FORAGING ECOLOGY OF FEMALE DALL'S SHEEP IN THE BROOKS RANGE, ALASKA

A

THESIS

Presented to the Faculty of the University of Alaska

in Partial Fulfillment of the Requirements

for the Degree of

DOCTOR OF PHILOSOPHY

By

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Fairbanks, Alaska

May 1996

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ABSTRACT

Most wild sheep (Ovis) are primarily diurnal. Thus, extreme cold, darkness, and limited quantities of low-quality forage during long winters above the Arctic Circle present a formidable challenge for sheep. Further, summer is particularly short at these high latitudes, providing little time for sheep to accumulate energy reserves for winter. This thesis discusses dietary and behavioral responses of wild sheep to the constraints of Arctic environments. Specifically, I determined diet composition and selection, forage quality, nutrient intake, and activity budgets of adult female Dall's sheep (ewes) (Ovis dalli dalli) near the northern extreme of the range of wild sheep for 2 years and constructed a model of the energy relationships of these animals.

Ewes primarily consumed forbs and grasses during summer, and strongly selected forbs over other forages in accordance with the predictions of optimal foraging theory. Diets primarily consisted of grasses in early winter, shifted to sedges in February, and back to grasses in early spring. Shrubs were consistently the least selected class of forage. When the diet was composed of forages with varying digestibility, microhistological analyses not corrected for differential digestibility were biased toward less digestible forage. Winter forage available to Dall's sheep in the northern Brooks Range was low in both digestibility and protein content.

In early summer ewes foraged during all hours of the day when sunlight was present for 24 hours. Sheep restricted their foraging almost entirely to daylight hours near the equinoxes, and foraged during all available hours of light, as well as 2.8 hours of the

night in December. Daily foraging time varied from 12.9 hours in June to 7.9 hours in December, and, when measured on a daily basis, was positively correlated with average windchill and daylength. Ash-free fecal nitrogen and in vitro digestible dry matter were most highly correlated with activity level on a monthly basis. Energetics modeling indicated that ewes were in a negative energy balance for 6-8 months each winter and lost nearly 30% of their body weight. Duration of the short summer growing period was most important for weight gain, and presence of deep snow determined weight loss in winter.

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ACKNOWLEDGMENTS

Support for this project was provided by the Alaska Department of Fish and Game, Arctic National Wildlife Refuge and the Alaska Fish and Wildlife Research Center of the U. S. Fish and Wildlife Service, Alyeska Pipeline Service Company, Boone and Crockett Club, Desert Bighorn Council-Ewes, Foundation for North American Wild Sheep, Institute of Arctic Biology at the University of Alaska Fairbanks, National Park Service - Alaska Region, National Rifle Association, Sacramento Safari Club, Mrs. P. A. Hansen, and Dr. D. F. Hallock.

I thank many people for their help during the process of completing work for Chapter 1 including: R. D. Guthrie for providing access to his captive Dall's sheep; K. R. Whitten and T. R. McCabe for assisting with animal capture; W. Eastland, W. Hansen, M. Hare, R. Kleinleder, J. Miller, T. Paragi, U. Petersen, C. Svendsen, and J. Woolington for help during collection of data; R. B. Harris for many helpful discussions and suggestions; and S. Amstrup, V. C. Bleich, D. J. Clark, T. R. McCabe, D. K. Rosenberg, R. J. Steidl, M. Udevitz, J. D. Wehausen, J. D. Yoakum, and 2 anonymous reviewers for comments on earlier versions of this chapter. G. W. Garner was instrumental in initiating the satellite telemetry portion of the work described in Chapter 1. Both he and S. G. Fancy, as coauthours, provided assistance in study design, use of satellite telemetry equipment, and aid in data analysis.

During work on Chapter 2, J. Thompson and L. Painter of Oregon State University Range Department provided help and advice on the domestic sheep portion of

this project and allowed us to use their domestic ewes. Coauthors J. P. Perkins, A. M. Ellingson, and T. J. Grubert all assisted in data collection on the domestic ewes portion of of this chapter and helped with data analyses. We appreciate the assistance of W. Eastland, W. Hansen, R. B. Harris, J. Miller, and J. Woolington during Dall's sheep data collection. And we thank R. T. Bowyer, D. M. Leslie, Jr., R. J. Steidl, and J. D. Wehausen for helpful comments on earlier versions of this chapter.

On Chapter 3, the assistance of B. Cazell, W. Eastland, D. Frugé, W. Hansen, M. Hare, R. B. Harris, Ø. Holland, R. Kleinleder, J. Miller, T. Paragi, U. Petersen, M. Petrula, C. Svendsen, M. Tempelton, and J. Woolington during data collection was greatly appreciated. And R. J. Steidl provided helpful statistical advice.

For Chapter 4, I appreciate the assistance of B. Cazell, W. Eastland, D. Frugé, W. Hansen, M. Hare, R. B. Harris, Ø. Holland, R. Kleinleder, J. Miller, T. Paragi, U. Petersen, M. Petrula, C. Svendsen, M. Tempelton, and J. Woolington during data collection. S. G. Fancy, D. D. Roby, R. J. Steidl, and J. D. Wehausen provided helpful statistical and analytical advice.

I especially thank my graduate advisor, D. R. Klein, who provided sound advice, guidance, and encouragement throughout the project, but particularly as coauthor on Chapters 3 and 4. I appreciated my graduate committee E. H. Follmann, G. W. Garner, E. C. Murphy, W. L. Regelin, L. A. Reneker, S. Thompson, and R. G. White for their help and patience throughout the process of completing this endeavor. And the cheerful help

of Norma Mosso and the rest of the staff at the Alaska Cooperative Fish and Wildlife Research Unit and Institute of Arctic Biology were invaluable and greatly appreciated.

And finally, I'd like to thank my family for their support and encouragement. But, most of all I appreciate patience of my wife, Wendy, who listened to my problems, helped me through the long years of lab analyses, and finally gave me the impetus I needed to end the procrastination and complete the writing of this dissertation.

INTRODUCTION

Wild sheep have generally been considered diurnal animals. Yet, Dall's sheep (Ovis dalli and ancestors) apparently have been resident for more than 125,000 years in the Brooks Range of Alaska (Korobitsyna 1974) -- a region that is characterized by long winters that include extended periods of darkness. Extreme cold and low-quality forage often available in limited quantities above the Arctic Circle in winter present further challenges to these large herbivores. Further, the growing season of forage plants is particularly short at these high latitudes, providing little time for sheep to accumulate energy reserves for winter. Despite these environmental factors, the Brooks Range contains large numbers of Dall's sheep, often at high densities (Summerfield 1974, McDonald et al. 1990). Consequently, this investigation focused on the adaptations that allow these most northern wild sheep to survive the extreme physical and energetic constraints above the Arctic Circle.

One possible avenue for behavioral adaptation is through selection of foraging areas and forage species. To have persisted under such harsh environmental conditions over time suggests that these animals should have developed foraging habits that optimize their use of the available resources (Pyke et al. 1977, Owen-Smith and Novellie 1982). A comprehensive study of foraging behavior and food habits of the closely related Stone sheep (O. d. stonei) was conducted in similar habitats in northern British Columbia, Canada, and concluded that forbs, the most nutritious and digestible forage in summer, were not selected -- an apparent deviation from optimal foraging theory (Seip and Bunnell

1985). Of the few foraging studies on Dall's or Stone sheep, only Ayres (1986) calculated selection indices, but these were based on availability values measured at local feeding sites and did not address selection at other levels. Further, although most of the studies used microhistological analyses of rumen or feces, none corrected for differential digestibility of forages in determining diet composition (Leslie et al. 1983, Holechek and Valdez 1985). Therefore, we investigated forage selection in summer near the northern extreme of the range of wild sheep in North America, where natural selection should exert its strongest pressure for optimal foraging, to determine if Dall's sheep also deviated from the predictions of optimal foraging theory.

Although, it is generally known that Dall's sheep primarily utilize wind-blown ridges for foraging and consume graminoids and willows (Salix) in winter (Murie 1944, Whitten 1975, Nichols 1978, Hoefs and Cowan 1979), only 1 previous study has focused on foraging ecology of Dall's sheep at similar latitudes (Ayres 1986), and it did not include winter. Consequently, species composition and nutrient content of Dall's sheep diets in winter above the Arctic Circle are poorly understood. Most information on diets and foraging of Dall's sheep comes from the warmer periods of the year and areas farther south with longer periods of daylight during winter (Hoefs 1975, Whitten 1975, Hoefs and Cowan 1979, Winters 1980, Heimer 1983, Elliott and McKendrick 1984).

Sheep also can adapt their diel activity to environmental conditions, such as day length, to minimize energy expenditure and maximize nutrient intake. Yet, due to logistical constraints, information on activity of Dall's sheep has been limited to the daylight hours, and consequently has included little information from winter (Whitten

1975, Hoefs and Cowan 1979, Winters 1980, Curby 1981). Winter-like conditions prevail for the greater part of the year above the Arctic Circle, and at the latitude of the study area the sun did not rise above the horizon for about 50 days (26 November - 16 January). Information on activity patterns and consequent energy budgets is essential to understanding how Dall's sheep cope with the extreme seasonal variations in forage availability, daylight, and temperature, particularly in winter when most adult mortality occurs (Murie 1944, Whitten 1975, Nichols 1978).

The only estimate of forage intake in winter has been for Stone sheep in northern British Columbia (Seip and Bunnell 1985), and so little is known about the quantity or quality of forage consumed by these sheep near the northern extreme of their range. Yet, this basic information is essential to understanding the relationship these animals have with their environment, and how changes in that environment affect them. Therefore, we designed this study primarily to obtain nutrient intake and information on energy expenditure from free-ranging adult female Dall's sheep (ewes) and use the information to construct a computer simulation model that could be used to predict changes in live weight and body composition under various environmental conditions. This model was then used to evaluate the relative effects of various input variables on weight gain and loss to determine to which parameters the model was most sensitive. The greatest value of this energetics model is to evaluate the current state of knowledge about Dall's sheep and their interactions with the environment, but it also can be used by land and wildlife managers to predict the effects of various management actions.

Chapter 1 presents the results of research designed to investigate methods to obtain data on the activity of Dall's sheep that could be used to quantify 24-hour activity budgets of these animals during the darkness of winter, which in turn could be used to derive energy budgets for subsequent modeling. Direct observations were used as a standard to evaluate the precision and accuracy of activity information obtained from conventional VHF radio transmitters and platform transmitter terminals (PTTs), which utilize near-earth satellites as signal receivers, each equipped with tip-switch motion sensors. Observations also are presented about both motion-sensor orientation and its effect on the ability to distinguish among animal behaviors, as well as the comparative costs of obtaining information on animal activity by direct observation, VHF telemetry, and satellite telemetry.

Chapter 2 presents the results of research designed to determine winter and summer rates of defecation (#/day) and excretion (g/day) of Dall's sheep ewes, which could later be used to calculate dry matter intake (DMI) for use in the energetics model. A protocol was developed using domestic ewes for calculating fecal excretion from information obtained by continuous observation and collection of feces in the field. The procedure involved separate determination of the 2 components of fecal excretion -- defecation rates and dry weight of an average defecation. We then applied the procedure to our data from Dall's sheep ewes to determine daily defecation and excretion rates during winter and summer.

Chapter 3 presents the results of research on seasonal changes in species composition and nutrient composition of Dall's sheep ewes diets. We used

microhistological analysis of fecal samples to estimate plant taxa in the diets. We also investigated the effect of differential digestibility of forage species on diet composition, and used correction factors to adjust initial composition estimates based on microhistological analyses. Forage samples were collected later based on these diets and used to construct simulated diets, which were then analyzed for nutrient content. These estimates then were used in conjunction with the estimates of fecal excretion to estimate energy and nitrogen intake on a seasonal basis. Forage taxa were also ranked by selection seasonally, and the effect of snow cover was evaluated in August and December.

Chapter 4 presents the results of research designed to estimate seasonal activity budgets of ewes near the northern extreme of their range. Information collected for Chapter 1 was used to ground-truth 24-hour activity data obtained from VHF radio transmitters, and to estimate specific behaviors from estimates of active and resting. Activity budgets were then used in conjunction with information on energy intake from Chapter 3 to produce a model of the annual energy budgets of these ewes. The model was calibrated with existing empirical data, a series of sensitivity analyses were performed, then the affect of changes in initial body weight and forage digestibility on winter survival was examined.

CHAPTER 1.
COMPARISON OF THREE METHODS FOR EVALUATING ACTIVITY OF DALL'S SHEEP[1]

ABSTRACT

Validation of the reliability of remote-sensing data is critical to subsequent analyses, yet is often neglected. Thus, we assessed the efficacy of 3 methods of collecting information on activities of captive and free-ranging Dall's sheep (Ovis dalli) in Alaska. Conventional very high frequency (VHF) radio-telemetry transmitters and platform transmitter terminals that transmit to satellites, each with motion-sensitive tip-switches, were compared with simultaneous direct observation. Both VHF (98% agreement) and satellite telemetry (98% agreement) reliably distinguished active from inactive behaviors for free-ranging females. For activity of a free-ranging male, rate of agreement with direct observation was lower ($P < 0.05$) by satellite telemetry (89%), but not by VHF telemetry (98%). Neither telemetry method could reliably distinguish standing from lying or feeding from walking. Satellite telemetry was most cost effective when a large amount of data was required from each animal. Direct observation was most cost effective when few samples were required from each animal and when access and visibility were good.

[1] Published as: Hansen, M. C., G. W. Garner, and S. G. Fancy. 1992. Comparison of three methods for evaluating activity of Dall's sheep J. Wildl. Manage. 56(4):661-668.

INTRODUCTION

Several methods have been used to measure activity of free-ranging wildlife. Early methods that rely on direct observation (Altmann 1974) continue to be used (Collins et al. 1978, Clutton-Brock et al. 1982, Jingfors 1982). Direct observation, however, is labor-intensive and impractical when visibility is poor or animals are sensitive to the presence of observers. Consequently, since it became available in the late 1960's, conventional very high frequency (VHF) radio-telemetry has been used to obtain information on activity of animals.

Conventional VHF transmitters have been used to measure activity in several ways, including inference of activity from changes in triangulated locations (Kammermeyer and Marchinton 1977, Woodruff and Keller 1982), presence or absence of a signal near a fixed point (e.g., nest, den, feeding site, water surface; Ralls and Siniff 1990), variation in amplitude of the radio signal (Hanley 1982, Althoff et al. 1989), and motion-sensing switches that vary the transmitted signal pulse-rate with collar movement (Knowlton et al. 1968, Georgii 1981, Garshelis et al. 1982, Shaffrey 1989). Recently, platform transmitter terminals (PTTs) were used to collect information about activities of free-ranging animals from motion-sensing switches via satellite (Fancy et al. 1988, Harris et al. 1990).

Few researchers have assessed the accuracy of information measured by motion sensors in VHF transmitters and most studies have used captive animals (Gillingham and Bunnell 1985, Green and Bear 1990, Kie et al. 1991); accuracy of VHF telemetry on free-

ranging animals has been reported only for white-tailed deer (Odocoileus virginianus; Beier and McCullough 1988). Accuracy of activity data for satellite telemetry has been examined for captive caribou (Rangifer tarandus), muskox (Ovibos moschatus), elk (Cervus elaphus), and mule deer (Odocoileus hemionus; Harris et al. 1990), and for 1 free-ranging muskox (Reynolds 1989). Although precise orientation of motion sensors within radio canisters can affect the ability to distinguish between activities (Harris et al. 1990), the orientation of sensors was not reported in most of these studies, and no comparisons of cost among the methods have been published.

We used direct observation as a standard to evaluate the precision and accuracy of data on the activity of Dall's sheep obtained from VHF transmitters and PTTs that were each equipped with tip-switch motion sensors. We also present observations about motion-sensor orientation and its effect on our ability to distinguish among animal behaviors, and about the comparative costs of obtaining information on animal activity by direct observation, VHF telemetry, and satellite telemetry.

STUDY AREA

We studied free-ranging Dall's sheep in the northern Brooks Range of Alaska (68.5° N, 149.3° W). The study area was primarily in the western portion of the Arctic National Wildlife Refuge, but included part of the Trans-Alaska Pipeline Corridor. Day length varied from 24 hours/day for about 60 days near the summer solstice, to no direct sunlight and only 3-4 hours of civil twilight daily for about 50 days near the winter

solstice. Daily temperature averaged 10 C in July and -29 C in January. Elevations ranged from 600 to 2,300 m. We were able to observe animals easily in the alpine tundra communities that predominated in the study area. Captive animals were held in a 40-m x 100-m fenced paddock near Fairbanks, AK.

METHODS

Data Collection

Each motion-sensitive tip-switch was parallel with the bottom of the radio canister (0°) and parallel with the animals spine to indicate up and down head movements in both VHF transmitters (Mod-500, Telonics, Mesa, Ariz.) and PTTs (CM 10001-004, Telonics, Mesa, Ariz.). We based motion-sensor orientation on data we obtained using a clinometer during observations of captive male Dall's sheep.

We placed 5 VHF transmitters (0.7 kg each) on free-ranging adult female Dall's sheep from October 1986 to June 1988. Tip-switches in these transmitters varied the signal period from 0.5 seconds when the animal's head was down, to 1.0 seconds indicating the animal's head was up. We used an omni-directional antennae, receiver, scanner, digital processor, and a dual-channel chart recorder geared to run at 0.4 m/hour (RA-5, TR-2, TS-1, TDP-2, and TDR-1, respectively; Telonics, Mesa, Ariz.), to record period and amplitude of transmissions from the VHF transmitters.

We obtained data on activity from satellite transmitters (1.9 kg) placed on 3 animals: 1 captive male from April to May 1986, 1 free-ranging male from October 1986

to October 1987, and 1 free-ranging female between October 1987 and October 1988. Rather than using the tip-switch to alter signal period, as with VHF transmitters, PTTs counted the number of seconds each minute during which the tip-switch was activated, and stored this number in a memory register (60-sec counter). Each new value of the 60-second counter was transmitted once per minute following an unmodulated carrier signal used to locate the transmitter by satellite (Fancy et al. 1988). PTT transmissions were picked up directly in the field by a satellite uplink receiver (Telonics, Mesa, Ariz.). Satellite telemetry collars also were equipped with separate VHF transmitters, thus allowing all 3 methods to be used simultaneously on these animals.

During data collection, we observed radio-marked animals for periods of 0.6-5.6 hours using binoculars or a spotting scope. We recorded the time of each behavior change. Both directly observed behavior changes and PTT 60-second counts were recorded directly on the strip chart so that data from all 3 methods used the same time scale to minimize time-lag errors. We covered these data when we analyzed the VHF telemetry data to avoid biased assessment of behaviors derived from VHF telemetry. Walking and running behaviors rarely lasted for >1 minute; longer instances of these behaviors for the captive male were caused by the observer to obtain 60-second counts.

We recorded 7 behaviors during our direct observations of free-ranging animals: running, walking, feeding, other active behaviors (e.g., social, comfort), standing, lying with head up, and lying with head down. Observations of the captive male also included lying and ruminating, and feeding at a trough.

Analyses

Calibration.--The VHF telemetry data were recorded as dot patterns on the dual-channel recorders. We based our classification of active or inactive behaviors on patterns of head up, head down, and signal amplitude reported in the literature (e.g., Gillingham and Bunnell 1985), and verified them visually in the field during data collection.

During field work, however, we noted that the length of time between behavior changes (bout length) for standing was much shorter than for either lying category, even though VHF telemetry signal patterns were similar. The distribution of activity-bout lengths was highly skewed, however, and could not be successfully transformed. Therefore, we used the Mann-Whitney U-test (Zar 1984:139) to determine whether length of behavior bouts could reliably distinguish between standing and lying.

We examined the PTT 60-second counts to determine which behaviors could be recognized as distinct. We used the 1-minute interval between PTT transmissions as our sample unit. No mixed behavior samples were used, and the 1-minute interval following each observed behavior transition was dropped from calibration analyses because of a lag between collection and transmission of sensor data inside the PTT. Because the variance of 60-second counts was not similar among behaviors and the distributions of counts for some behaviors were highly skewed, the Kruskal-Wallis test (Zar 1984:201) was used to determine whether PTT 60-second counts differed among individuals or behaviors. We also used the Mann-Whitney U-test to compare 60-second counts among specific

behaviors and individuals; for these comparisons, we adjusted the α-level by the Bonferroni method to achieve a family confidence level of $\alpha = 0.05$ (Neter and Wasserman 1974:146). All behaviors for the free-ranging sheep that could not be distinguished were combined into composite categories for subsequent validation analyses; no further analyses were performed on data from the captive sheep.

Validation.--We assessed the ability of each telemetry system to correctly classify an animal's behavior during a particular sampling unit (agreement). Agreement was used as a measure of the precision of later estimates of activity budgets because it measured the number of individual classification errors rather than whether more errors occurred during a particular behavior. To compare VHF telemetry data with direct observations, we first examined each strip-chart and marked each change in behavior. Then we randomly selected 20 1-second samples/hour from each chart and compared the behavior recorded for the bout within which each sample occurred with the behavior observed directly during that second. For satellite telemetry, we compared all available 60-second counts, including those with mixed behaviors, with the most prevalent behavior during the corresponding 1-minute of direct observation. We used 2 x 2 tables to compare the paired samples of behavior derived from direct observation with either VHF or satellite telemetry. Agreement was measured as the percent of observations falling in cells along the diagonal of the tables. The 95% confidence intervals based on asymptotic standard errors for Cohen's Kappa (Kraemer 1983) allowed statistical comparisons among the methods.

Finally, we assessed ability of each telemetry system to measure the relative amounts of time that animals spent performing each recognizable behavior (accuracy) during an extended period (activity budget). An activity budget was considered to be the percent of samples classified into each behavior category over the total sampling time. Bias was our measure of accuracy and was calculated as the difference between percent of samples classified as active by a telemetry method and by direct observation. Bias was considered positive when the telemetry method classified a sample as active when the sheep was observed to be inactive. We used McNemar's Symmetry Chi-square ($\underline{X_c}^2$) to determine whether observations in cells on either side of the diagonal (errors) were statistically equal (unbiased; Zar 1984:156).

Cost Comparison

We estimated costs of the 3 methods for an energetics study of Dall's sheep. The study required information on behavior from all 24 hours of the day and all seasons of a 1-year period. We considered both fixed and relative costs. Fixed costs were independent of the number of days of sampling (e.g., equipment costs, animal capture) and were divided by the number of animal-days of data required during the year. Cost of calibrating PTT 60-second counts was considered a fixed cost; validation of VHF telemetry classification criteria could be conducted during routine data collection, and was not considered an additional cost. Relative costs included personnel and supplies for 1 animal-day of data collection and these were divided by the probability of completing 24 hours of

data collection for each method. Cost per animal-day of data collected was the unit of measure for these comparisons.

Fixed costs (1990 estimates) included $1,000 for each animal captured; $350 for each VHF telemetry collar; $3,000 for VHF telemetry receiving equipment; $3,300 for each satellite collar; Argos data processing fee of $3,000 for 1 year; $10,500 for satellite uplink receiving equipment; and cost of personnel, transport, and supplies for 7 days to calibrate PTT 60-second counts. Relative costs included 2 workers at $10/hour for 12 hours each per day, $20/day for field supplies, and $20/day for transport to and within the study area. Probabilities of completing a 24-hour collection period were 0.5 for direct observation, 0.8 for VHF telemetry, and 1.0 for satellite telemetry (M. C. Hansen, unpubl. data).

RESULTS

VHF Telemetry vs. Direct Observation

Calibration.--We analyzed 1,008 simultaneous samples from 49 animal-hours of direct observation and VHF telemetry obtained from 5 female and 1 male free-ranging Dall's sheep. We could not reliably distinguish among feeding, walking, running, social, or comfort behaviors using data from VHF telemetry. Therefore, these were combined into a single category called active, which occurred when both amplitude and period of the VHF telemetry signal varied. Although standing and lying patterns of signal period and amplitude were similar, bout lengths for standing (median = 0.3 min, $n = 256$) and lying

(median = 19.1 min, $n = 24$) were different ($U = 372$, $P < 0.001$). The ranges of bout lengths for standing (0.1-12.9 min) and lying (0.4-87.1 min), however, overlapped substantially; of samples that were classified as standing by VHF telemetry, only 44% from the female and 43% from the male were correct (Table 1). Furthermore, lying with head down occurred infrequently. Therefore, we combined standing and both categories of lying into a category called inactive which occurred when both signal amplitude and period were constant.

Validation.--For the combined behavior categories of active and inactive, we observed 98% agreement for both the female and male sheep (Table 2). The 95% confidence intervals around Cohen's Kappa indicated that agreement did not differ by sex (Table 2). Error rates when sheep were observed active were 0.8% for the female and 0.0% for the male; error rates while inactive were 5.3% for the female and 5.2% for the male. Most errors occurred when we observed the sheep to be standing, but VHF telemetry signals indicated the sheep was active (Table 1). Consequently, activity budgets estimated by VHF telemetry for our sampling periods were biased slightly toward active (Table 2); yet, only for the male was bias different from zero ($X_c^2 = 4.0$, $P = 0.046$, $n = 172$). Our sampling periods for the female, however, were heavily weighted toward active behaviors (78%) compared to the male (55%). On a 24-hour basis, female sheep in this population spent only 56% of their time active in summer and 34% in winter (M. C. Hansen, unpubl. data). If 56% of our sampling periods had been from active sheep, agreement rates would not have changed for either sex, but bias for the female would have

Table 1. Agreement between random paired samples of behavior classifications obtained by direct observation and VHF telemetry for Dall's sheep in the Brooks Range, Alaska, 1986-88.

Sex	Activity derived by VHF telemetry					
Observed				Lying		Percent
activity	Active[a]	Inactive[b]	Standing	Head up	Head dn	agreement
Females						
Walking	13					100
Feeding	631		4	1		99
Standing	9	8	16	3		44
Lying head up	1	13	1	136		90
Male						
Walking	19					100
Feeding	76					100
Standing	4	11	12	1		43
Lying head up		2	1	43	1	91
Lying head down					2	100

[a] Recorded when animal was active but unsure whether feeding or walking.

[b] Recorded when animal was inactive but unsure whether standing or lying.

Table 2. Two x two tables of paired classifications of Dall's sheep behavior, agreement, Cohen's Kappa coefficient, and bias obtained simultaneously by direct observation, VHF telemetry, and satellite telemetry in the Brooks Range, Alaska, 1986-88.

Sex	Direct observation			Agreement	
Method	Active	Inactive	(%)	Kappa[a]	Bias
Female					
VHF (n = 5)					
Active	644	10	98	0.95 A	+0.6
Inactive	5	177			
Satellite (n = 1)					
Active	151	2	98	0.93 A	0.0
Inactive	2	35			
Male					
VHF (n = 1)					
Active	95	4	98	0.95 A	+2.3 *
Inactive	0	73			
Satellite (n = 1)					
Active	30	8	89	0.68 B	-2.3
Inactive	12	124			

[a] Kappa coefficients with the same letters do not differ ($P > 0.05$).

* McNemar Symmetry Chi-square test of the null hypothesis that bias is equal to zero ($P < 0.05$).

increased to 1.9% and been different from zero ($\underline{X_C^2}$ = 10.7, $\underline{P}$ = 0.001, $\underline{n}$ = 836). Simulating winter activity rates also indicated no change in agreement rates, but bias for both sexes increased to 3.5% and differred from zero ($\underline{X_C^2}$ = 23.5, $\underline{P}$ < 0.001, $\underline{n}$ = 836 for the female; $\underline{X_C^2}$ = 6.0, $\underline{P}$ = 0.014, $\underline{n}$ = 172 for the male).

Satellite Telemetry vs. Direct Observation

Calibration.--We obtained 562 simultaneous direct observations and PTT 60-second counts from 1 captive male sheep, 174 from 1 free-ranging male, and 190 from 1 free-ranging female sheep. Of these, 98 (17%) paired samples from the captive male, 20 (11%) from the free-ranging male, and 54 (28%) from the free-ranging female were dropped from the calibration phase of analyses because of mixed behaviors.

For paired samples of pure behaviors, 60-second counts for the captive male were highest for running and moderately high for feeding at a trough (Table 3). We could not distinguish any other specific behaviors by their 60-second counts (Table 3). For all 3 animals, counts were similar for all inactive and feeding categories, but variation was higher for feeding (Table 3). Except for feeding on the ground by the captive male, counts were higher for active behaviors than for inactive behaviors for all 3 animals (Table 3). Resulting composite behaviors analyzed in the subsequent validation phase were inactive when 60-second counts were 0-1, active when counts were 2-49, and running when counts were >50.

Table 3. Mean number of seconds with tip-switch activation per minute (60-sec counts) for specific behaviors obtained from satellite telemetry of 1 male and 1 female free-ranging Dall's sheep in the Brooks Range, Alaska, and of 1 captive male Dall's sheep in Fairbanks, Alaska, 1986-88.

	Free-ranging						Captive		
Observed	Female			Male			male		
behavior	x	SD	n	x	SD	n	x	SD	n
Lying head down	0.0A[a]	0.0	6	0.2AB	0.8	13	0.0AB	0.0	6
Lying head up	0.0A	0.0	23	0.1A	0.6	96	0.0A	0.5	293
Lying ruminating							0.0A	0.0	20
Standing				1.0B	1.6	17	0.7B	2.6	76
Feeding on ground	20.4B	11.3	107	5.6C	6.5	27	1.5BC	1.2	5
Feeding at trough							13.5D	7.8	28
Walking				4	-	1	4.3C	5.2	25
Running							53.6E	11.1	11

[a] Means within columns with same letters do not differ (Mann-Whitney U-Tests; $P > 0.05$ for family of comparisons).

Validation.--Agreement between data from direct observation and satellite telemetry for the free-ranging female was high and similar to agreement between data from direct observation and VHF telemetry for both sexes (Table 2). Agreement between data from direct observation and satellite telemetry was lower for the free-ranging male than for the female, however, and lower than for VHF telemetry for both sexes (Table 2). For the male, error rate while inactive was 6.2% and errors were caused by either head movement while standing or shifts between inactive categories; error rate while active was 29% and most errors occurred when the male fed without lifting his head for the entire minute. The number of errors during active and inactive behaviors for both free-ranging sheep nearly balanced each other in our samples, resulting in unbiased estimates of activity budgets (Table 2). Simulating the diel activity rates of wild female sheep indicated that agreement rates would be similar, but bias would increase slightly in summer (2.1%) and would be different from zero in winter (bias = 3.2%; $\underline{X_C}^2 = 4.5$, $\underline{P} = 0.034$, $\underline{n} = 190$). For the male, simulated agreement rates did not change for summer or winter activity budgets, but bias increased and was different from zero for summer (13.2%; $\underline{X_C}^2 = 16.0$, $\underline{P} < 0.001$, $\underline{n} = 174$) and winter (5.7%; $\underline{X_C}^2 = 4.2$, $\underline{P} = 0.041$, $\underline{n} = 174$).

Cost Comparison

Nearly all costs for direct observation were for personnel and supplies and were the same whether 1 individual was observed for 2 days or 2 individuals for 1 day each. The cost for each animal-day of data collection for direct observation was constant at

$540/animal-day, and increasing the number of individual animals monitored did not affect the cost for each animal-day of data. Our study did not require data from specific individuals; such a requirement would increase costs by adding time to locate specific individuals or necessitate the use of VHF transmitters.

Both telemetry methods included fixed costs associated with radio equipment and capture of animals. Therefore, cost per animal-day declined almost logarithmically as the number of animal-days of collection per individual animal increased. Concomitantly, direct observation was most cost effective when few days were required for each monitored animal (<9 days). Satellite telemetry did not require personnel in the field after capture of animals and calibration of 60-second counts were completed. Therefore, cost per day continued to decline as days of data collection per monitored animal increased, making satellite telemetry the most cost effective method when large amounts of data (>19 days) were required for each animal. Cost per day for VHF telemetry began to level off at about 20 days of data/monitored animal as a result of costs associated with keeping personnel in the field during data collection; this method was only slightly more cost effective than the others when 9-19 days of data were required for each animal.

DISCUSSION

VHF Telemetry

The VHF telemetry method provided a good means of determining whether an animal was active or inactive, and obtaining general activity budgets. Our agreement rates

(female = 98%, male = 98%) were similar to those reported for white-tailed deer (active = 98%, bedded = 96%; Beier and McCullough 1988) and elk (94%; Green and Bear 1990) using head up and down tip-switches. Our activity budgets obtained from tip-switches and VHF telemetry seemed more accurate (bias = 1-4% for the female, bias = 2-4% for the male) than those reported for chamois (Rupicapra rupicapra; 95% correspondence; Hamr and Czakert 1986), black-tailed deer (Odocoileus hemionus columbianus; 91% correspondence; Gillingham and Bunnell 1985), and mule deer (R^2 = 0.97; Kie et al. 1991). This may be, in part, because increasing the length of time upon which a classification is based increases accuracy (Beier and McCullough 1988). We used long periods of continuous data (0.6-5.6 hr) for our classifications, and only later tested their precision and accuracy with random 1-second samples.

Most bias and about half of the errors for VHF telemetry resulted from tip switch activation caused by head movements while animals were standing. The slight bias of activity budgets toward active may be eliminated by slightly lowering the posterior end of the tip switch (-2°) to limit activation of the switch by head movements while the animal is standing. Lowering the posterior of the tip switch 4° or more, however, may restrict its activation when animals feed on plants above themselves on a slope, thus making it more difficult to distinguish this behavior from inactive.

Satellite Telemetry

Satellite telemetry allowed us to determine whether the female was active or inactive as accurately and precisely as did VHF telemetry. For the male, however, satellite telemetry was less accurate and precise than VHF telemetry. Most errors resulted when the male sheep rested its head on the ground while lying and when it fed with its head down for durations >1 minute. These behavior patterns occurred more often with the male than the female, and were probably sex-related; they likely occurred because the large horns of males are much heavier than those of females, and because males may be less vigilant than females due to larger body size (Underwood 1982, Berger and Cunningham 1988) and lack of lamb-rearing responsibilities. Low rates of agreement of 60-second counts, similar to those we noted for the male sheep, were reported for elk and were attributed to counts of zero when feeding (Harris et al. 1990). For several other species, agreement rates for active and inactive behaviors were similar to those we noted for the female sheep, but for caribou and moose (Alces alces), walking could usually be distinguished from feeding (Harris et al. 1990).

Adjustment of the tip-switch angle may allow walking to be distinguished from other active behaviors for Dall's sheep. Work on mule deer (Harris et al. 1990) suggests that for ungulates that hold their neck erect, a tip-switch angle of +6° to +10° might improve the distinction between feeding and walking behaviors. Furthermore, as with VHF telemetry, increasing the length of sampling periods improves precision and accuracy of predicted behavior and number of behaviors that can be recognized (Harris et al. 1990).

When a large number of 60-second counts during known behaviors is available, an algorithm can be used that compares the pattern of all 60-second counts received during a satellite overpass (i.e., 4-12 consecutive counts) with the distribution of counts received during known behaviors (Harris et al. 1990). Such an approach probably would have eliminated most of the errors that caused high bias rates for the male sheep. The algorithm combines several consecutive 60-second counts, however, and applies the resulting behavior to a time unit that is several minutes long. Thus, the algorithm would not recognize behaviors that occur for short durations, such as standing and running.

MANAGEMENT IMPLICATIONS

Direct observation had little or no error associated with it and could be used to recognize very specific animal behaviors. Direct observation is not practical, however, for animals that live in areas where visibility is limiting (e.g., dense vegetation, Arctic winter), move rapidly or extensively, or are sensitive to the presence of observers. Furthermore, direct observation can be prohibitively expensive when large sample sizes are required and when study design requires repeated observation of specific individuals.

Conversely, the VHF telemetry method can be effective under conditions that inhibit direct observation or present unsafe or uncomfortable conditions for researchers, and is less costly than direct observation when large sample sizes are required from each monitored animal. Primary drawbacks of VHF telemetry are that only general behaviors can be distinguished, a large, initial financial investment is required, and capture and fitting

of animals with collars may affect behavior or cause stress or discomfort (Bleich et al. 1990).

Satellite telemetry has many of the advantages of VHF telemetry, but can provide data under even more adverse conditions than VHF telemetry and be less costly than VHF telemetry when large sample sizes are required from each monitored animal. PTTs used in this study were set to transmit for 6 hours at 24 hour intervals, but other systematic sampling designs easily can be programmed (e.g., transmit 24 hr at 4-day intervals). Furthermore, animal location and other information, such as ambient temperature, can be acquired with little additional cost (Fancy et al. 1988, Harris et al. 1990). Disadvantages of satellite telemetry are that it requires the largest initial financial investment of the 3 methods, fewer satellite overpasses occur at lower latitudes, especially around local midnight, and PTTs are heavier than VHF transmitters and may have greater affects on behavior or cause more stress or discomfort (Bleich et al. 1990).

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CHAPTER 2.

DAILY FECAL EXCRETION AND DEFECATION RATES OF FREE-RANGING DALL'S SHEEP CALIBRATED USING DOMESTIC SHEEP[2]

ABSTRACT

We used metabolism crates to determine hourly rates of defecation and fecal excretion for 4 nonreproductive domestic ewes (Ovis aries) during 4 consecutive 24-hour periods. From these data on domestic ewes, we developed a protocol for analyzing focal animal observation periods of <24 hours to determine daily rates of defecation and fecal excretion for free-ranging adult female Dall's sheep (ewes) (O. dalli dalli) in Alaska. Mean daily rate of excretion for domestic ewes was 720 g/day (SE = 26.1, n = 16). Number of defecations / hour averaged 1.12 (SE = 0.06), with a mean weight / defecation of 26.8 (SE = 1.00) g . Factors affecting hourly rates of excretion for domestic ewes were individual differences, percent of the hour spent standing, number of transitions from bedding to standing, and hour of the day. Together these factors explained less than one-half the variability of the data set ($R_a^2 = 0.41$, n = 384). Regression analyses indicated the effect of time since last defecation on oven-dry weight / defecation was also significant (t = 4.00, P < 0.001, n = 424), but not highly correlated ($R^2 = 0.034$). Number of

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[2] Prepared for publication as: Hansen, M. C., J. P. Perkins, A. M. Ellingson, and T. J. Grubert. 1996. Daily fecal excretion and defecation rates of free-ranging Dall sheep calibrated using domestic sheep. J. Wildl. Manage. 00(0):000-000.

defecations per hour for Dall's sheep ewes was higher in summer ($\bar{x}$ = 1.67, SE = 0.36, n = 15) than in winter ($\bar{x}$ = 0.69, SE = 0.18, n = 13; t = 2.31, P = 0.03), but mass per defecation (dry weight) during summer ($\bar{x}$ = 15.0, SE = 1.04 g, n = 33) was not different from winter ($\bar{x}$ = 15.9, SE = 1.15 g, n = 12; t = 0.458, P = 0.649). Daily rates of defecation calculated from these estimates were 40.0 defecations/day in summer and 16.6 in winter, and daily fecal excretion (dry weight) was estimated to be 612 g/day in summer and 254 g/day in winter. Finally, we used interpolation based on number of hours Dall's sheep ewes spent feeding to estimate fecal excretion during the remainder of the year. The low excretion rates for ewes during winter probably resulted from low forage digestibility and availability; and, together with the observation that Dall's sheep ewes lost weight, indicate that winter diets were sub-maintenance.

INTRODUCTION

Estimates of daily fecal excretion by free-ranging animals are useful in calculations of intake of forage, minerals (Belovsky and Jordan 1981), trace nutrients, and soil (Arthur and Aldredge 1979, Miquelle 1983) and for calibrating pellet-group indices of animal abundance (Rowland et al. 1984, Fuller 1991). Daily fecal excretion has been reported for penned mule deer (Odocoileus hemionus; Dietz et al. 1962), and for both penned and free-ranging moose (Alces alces; Belovsky and Jordan 1981, Miquelle 1983, Joyal and Ricard 1986). Other studies of free-ranging mule deer (Arthur and Aldredge 1979, 1980) and white-tailed deer (O. virginianus; McCullough 1982) relied on defecation rates (# of

defecations / day) derived from penned animals to calculate fecal excretion rates (weight of excretia / day). Defecation rates have been obtained from several species of penned ungulates (e.g., Neff 1968, Dinerstein and Dublin 1982, Rollins et al. 1984), and from free-ranging white-tailed deer (Rogers 1987), elk (Cervus elaphus; Collins and Urness 1979), and moose (Belovsky and Jordan 1981, Miquelle 1983, Joyal and Ricard 1986).

Most studies assume rates of fecal excretion vary diurnally, and define 1 day as their sampling unit. A continuous sampling period of 24 hours is difficult under most field conditions, and in part may be responsible for the paucity of literature on fecal excretion from wild ungulates. Nonetheless, excretion rate is primarily dependent on forage digestibility (Church 1976), which does not vary diurnally for most ungulates. Physiological research shows that although a diurnal pattern of digesta flow is apparent in the upper digestive tract of domestic sheep, the pattern is lost through delays and reduction of digesta volume prior to reaching the large intestine, even under the extreme case of 1-2 meals/day (Goodall and Kay 1965, Topps et al. 1968). Furthermore, models based on data from domestic sheep fed only twice per day suggest that diurnal variation of fecal excretion should occur, but increased time to break down long forage fibers of dried grass in the rumen would dampen the hourly variation to within 4% of the mean (Blaxter et al. 1956). Indeed, when domestic sheep were fed a highly digestible, finely ground, pelleted ration, diurnal variation in hourly excretion rates was predicted to be only 16% above or below the mean (Blaxter et al. 1956).

Although supply of excretia to the colon should be relatively constant, animal behavior may affect rates of defecation and excretion. Collins and Urness (1979) noted that elk defecated more often when traveling, and most ruminants defecate after arising from a resting period (Church 1976:117). Further, defecation and excretion rates may differ between penned and free-ranging animals because forage digestibility and availability, as well as activity, are usually different for penned and free-ranging animals (Rogers 1987).

We attempted to determine defecation and excretion rates of Dall's sheep ewes in the Brooks Range, Alaska during winter and summer by a continuous observation and complete collection of feces procedure. We encountered difficulty in locating and collecting all defecations within observation periods, however, and were not able to obtain collection periods during hours of darkness. We then developed a protocol for collecting fecal information on excretion in the field and used data from penned domestic ewes to determine adequate sample sizes for the 2 components of fecal excretion -- defecation rates and dry weight of the average defecation. Further, we tested the hypotheses that rates of fecal excretion and defecation did not vary diurnally, and that hourly fecal excretion and defecation rates were not different for active and resting behaviors for domestic ewes. We then applied the procedure to our data from Dall's sheep ewes to determine daily rates of defecation and excretion during winter and summer.

STUDY AREA

We conducted experiments with domestic sheep at the Department of Animal Sciences Facility, Oregon State University, Corvallis. Field work with Dall's sheep was conducted in the northern Brooks Range, Alaska (68.5° N, 149.3° W), primarily within the western boundary of the Arctic National Wildlife Refuge. Day length varied from 24 hours/day for about 60 days near the summer solstice, to no direct sunlight and only 3-4 hours of civil twilight daily for about 50 days near the winter solstice. Daily temperature at the study site averaged 10 C in July and -29 C in January during our experiments. Elevations where we observed ewes ranged from 600 to 1,400 m, and vegetation in these areas consisted primarily of alpine tundra that afforded good visibility for behavioral observations.

METHODS

Domestic Sheep

One 3-year-old Coopworth ewe and three 4-year-old Coopworth-PolyPay cross ewes ($\bar{x}$ = 66, SE = 1.7 kg) were used in feeding trials. None of these animals was pregnant or lactating. The animals were kept in a large pen and fed long grass hay and corn for 2 weeks prior to initiation of our work in January 1994. For 3 days prior to our 4-day trial, and during the trial, each animal was confined to a 0.5 m by 2 m metabolism crate and fed 0.68 kg of the same long grass and 0.23 kg of a pelleted alfalfa ration (Table 4) twice per day (0900 and 1700 hr). Water was provided ad libitum. We visually

Table 4. Crude protein (%; CP), crude fat (%; CF), neutral detergent fiber (%; NDF), acid detergent fiber (%; ADF), acid detergent lignin (%; ADL), in vitro dry matter digestibility (%; IVDMD), and gross energy (cal/g; GE) of the diet fed domestic ewes during fecal excretion trials at Oregon State University, 1994.

Forage	CP	CF	NDF	ADF	ADL	IVDMD	GE
Long Grass Hay	9.21	2.13	65.40	37.23	2.59	51.9	4320
Alfalfa Pellets	20.98	1.98	53.31	37.05	11.36	61.5	4579

monitored each animal 24 hours/day during the trial and recorded the time to the nearest minute at which each animal stood up or laid down and the time of each defecation. Pellets were captured in individual trays for each ewe and removed immediately after each defecation. Each pellet group was bagged individually, labeled, oven-dried at 60° C to a constant weight, and then weighed to the 0.1 g.

We noted that ewes frequently defecated after standing from a bedded position. Consequently, we used analysis of variance and covariance (Neter and Wasserman 1974) to test for the effects of standing and lying behaviors on defecation rate by recording for each ewe and each 1-hour period of trial the number of transitions from lying to standing and the proportion of each hour spent standing. These 2 continuous variables were used as covariates and individual ewe, day of trial, time of day, and period of day were used as

categorical factors in repeated-measures analysis of variance (Wilkinson 1990) to test effects on weight of feces excreted. Period of day was defined as morning (0701 - 1300 hrs), afternoon (1301 - 1800 hrs), evening (1801 - 2300 hrs), and night (2301 - 0700 hrs), and was not used in the same model as time of day. Lowess smoothing (Wilkinson 1990) was used to aid in defining periods of day. We also used multiple regression (Neter and Wasserman 1974) to test for effect of elapsed time between defecations by calculating weight of each defecation and number of minutes since the previous defecation.

Estimates of required sample sizes were derived by sequentially plotting mean excretion rate and 95% confidence interval of each ewe against number of hours sampled, similar to the procedure of Odum and Kuenzler (1955). Under field conditions, however, it is often not possible to collect every defecation observed. Therefore, we also tested an alternative sampling strategy wherein number of defecations per hour was derived by direct observation, and then multiplied by mean weight per defecation derived from a sample of defecations.

Dall's Sheep

Wild and free-ranging Dall's sheep ewes were observed using binoculars and a spotting scope at distances of 40 to 400 m. Summer observations were made in June and July 1987 at which time 85% of observed ewes were lactating. Winter observations were made in February and April 1988, at which time most ewes were probably in mid-pregnancy. Individual ewes undisturbed by our presence were observed continuously for

1.5 to 7.8 hours ($\bar{x}$ = 3.2, SD = 2.1 hr) between 1200 and 2000 hours Alaska Standard Time. Only those observation periods that included both bouts of foraging and resting behavior were used in analyses because marked differences in defecation rate are associated with different behaviors (Church 1976:117, Collins and Urness 1979). Times and locations of defecations and changes in behavior were noted.

Feces were collected from Dall's sheep ewes as soon as possible after defecation without disturbing the animals. Fecal samples were later oven-dried at 50° C to a constant weight: this was different than the 60° C used for domestic ewes due to local availability of drying equipment. In addition, 20 pellets from each defecation were weighed as a group to the nearest 0.1 g to determine mean mass of pellet.

We were not able to collect all defecations observed during observation trials in the field and so used the alternative strategy of calculating number of defecations per hour from the observation trial and supplemented the calculations of weight per defecation with additional fecal groups collected immediately before and after the trial. Estimates of required sample sizes for Dall's sheep ewes also were derived by sequentially plotting mean excretion rate and 95% confidence interval of each ewe against number of hours sampled, similar to the procedure of Odum and Kuenzler (1955). The Mann-Whitney U test was used for comparisons between seasons when assumptions for the two sample t-test could not be met.

We compared our estimates of daily fecal excretion with estimates for other ungulates from the literature. To compensate for differences in weight between studies

and seasons, we converted all estimates to a per kg body weight$^{0.75}$ basis. Live body weights of Dall's sheep ewes of 68.8 kg (SE = 1.71, n = 5) in October and 56.0 kg (SE = 1.00, n = 3) in March were obtained from similar ewes in the study area during capture for a concurrent radio-telemetry study.

We also interpolated between our estimates of winter and summer excretion and defecation rates to provide values for the remainder of the year. Both rates of excretion and forage intake are correlated with forage digestibility (Church 1976). Consequently, we used time spent foraging by free-ranging Dall's sheep during 8 months of the year (Chapter 4), as an index to forage intake to calculate estimates of excretion and defecation rates by a simple ratio method:

$$EXCR_{MonthX} = (EXCR_{Winter}) + \left[(EXCR_{Winter} - EXCR_{Summer}) \times \left(\frac{FT_{MonthX} - FT_{Winter}}{FT_{Summer} - FT_{Winter}} \right) \right],$$

where EXCR was fecal excretion rate and FT was hours spent feeding. We used a level of significance of $\alpha = 0.05$.

RESULTS

Domestic Sheep

Factors Affecting Excretion Rate.--Overall, the mean daily rate of excretion for domestic ewes was 720 g/day (SE = 26.1, n = 4) (Table 5). There were marked differences in mean excretion rate among individual ewes ($\bar{x}$ = 818, SE = 17.9; $\bar{x}$ = 608, SE = 11.2; $\bar{x}$ = 642, SE = 15.0; and $\bar{x}$ = 811, SE = 27.6 g/day), and consequently, the

Table 5. Summary of daily excretion of fecal dry matter by Dall's sheep ewes in Alaska, bighorn sheep in British Columbia, mule deer in Colorado, and domestic sheep fed various diets.

			Excretion (g)	
Reference	Species	Diet	Whole animal	Per kg body wt.$^{0.75}$
This study	Dom. ewes	Grass hay / Alfalfa pellets	720	31.1
	Dall's sheep	Dry graminoids (Winter)	254	12.3
	Dall's sheep	Green forbs and graminoids (Summer)	612	29.9
Hebert	Bighorn sheep	Alpine forage	343	15.2
(1973)	Bighorn sheep	Early Agropyron hay	472	20.9
	Bighorn sheep	Late Agropyron hay	520	22.9
Dietz et al.	Mule deer	Mt. mahogany	170	12.3
(1962)	Mule deer	Alfalfa	540	38.9
Church	Dom. sheep	Alfalfa pellets	480	34.6
(1976)	Dom. sheep	Concentrate ration	150-250	10.8-18.0

effect of individual ewe in the ANOVA was significant ($F = 33.91$, $P < 0.001$, $R^2 = 0.894$, $df = 3$). Measured on an hourly basis, mean rate of excretion was 30.0 g/hour ($SE = 1.1$). Although still a significant factor ($F = 4.61$, $P = 0.004$, $df = 3$), ewe individuality explained little of the overall variability in hourly excretion ($R^2 = 0.035$). Excretion rate, however, was not correlated with body weight ($t = 0.225$, $P = 0.843$, $R^2 < 0.001$, $n = 4$).

Defecation immediately after rising from a period of bedding was common. Ewes defecated within 1 minute of 50.8 % of all transitions from bedding to standing, and we observed both domestic ewes and Dall's sheep ewes defecate up to 4 times within a 30 minutes of terminating a long resting period. Furthermore, 36.7 % of all defecations occurred within 1 minute of such a transition from bedded to standing, whereas only 1.2 % of defecations occurred within 1 minute of a transition from standing to bedding (Fig. 1). We also noted that ewes defecated more frequently when standing longer than 1 minute (54.7 % of all defecations) than when bedding longer than 1 minute (7.4 %). Although the effects of percent of the hour spent standing ($t = 3.93$, $P < 0.001$, $R^2 = 0.036$) and number of transitions to standing ($t = 4.49$, $P < 0.001$, $R^2 = 0.048$) were significant, they explained little of the overall variability.

Of temporal factors examined, neither day of trial ($F = 0.35$, $P = 0.791$) nor period of the day ($F = 2.25$, $P = 0.083$) had a significant effect on hourly rate of excretion. Ewes, however, excreted slightly less during night ($\bar{x} = 25.8$, $SE = 1.72$ g/hr) than during morning ($\bar{x} = 33.0$, $SE = 2.09$ g/hr), afternoon ($\bar{x} = 31.3$, $SE = 2.85$ g/hr), and evening ($\bar{x} = 30.7$, $SE = 2.12$ g/hr). Morning, afternoon, and evening were not different from

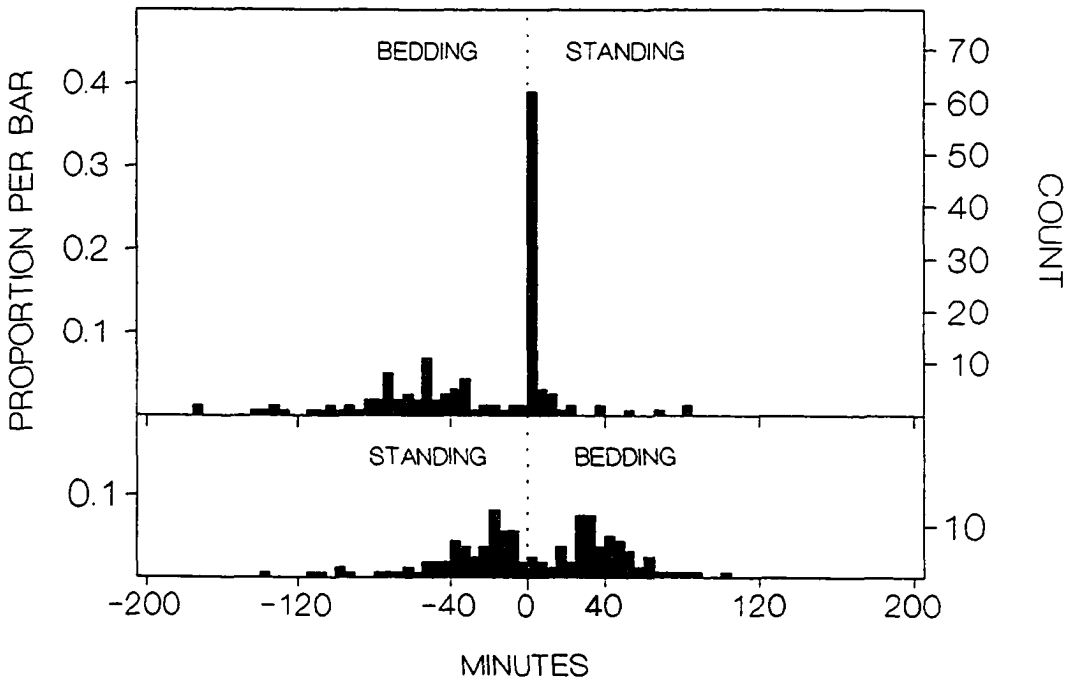

Fig. 1. Frequency of defecations by 4 female domestic ewes prior to and following behavior transitions from bedding to standing (above) and from standing to bedding (below) at Oregon State University, 1994.

each other ($F = 0.28$, $P = 0.754$), but when the night period was compared with the combined 3 remaining periods of the day the difference was significant ($F = 6.135$, $P = 0.014$, $R^2 = 0.016$). Hour of day, however, had a more significant effect on excretion rate ($F = 1.95$, $P = 0.006$, $R^2 = 0.111$) than did period of the day. When individual ewe, percent of the hour spent standing, number of transitions to standing, and hour of day were combined in the model, they collectively explained 41% of the variability in these data. Effect of hour of day resulted from elevated defecation rates associated with increases in proportion of time spent standing at 1000, 1400, and 1700 hours (Fig. 2). Two of these 3 hourly periods occurred soon after the ewes received new feed. When data for these 3 hours were removed from the model, the results were no longer significant ($F = 1.18$, $P = 0.268$). Further, there was a significant interaction between day and hour ($F = 1.82$, $P = 0.001$), indicating that differences across hours in some days were reversed in other days.

The relationship between weight of each defecation and time since the previous defecation was significant ($t = 4.00$, $P < 0.001$), however, it explained little of the variability in weight of defecations ($R^2 = 0.034$). Effect of behavioral state when defecating was also significant ($F = 17.72$, $P < 0.001$), and explained more of the overall variability ($R^2 = 0.111$).

Estimation of Sample Size. --For continuous sampling, where all defecations could be collected, plots of mean hourly rate of excretion showed that stable means for each of the 4 ewes were reached between 15 and 20 hours of sampling (Fig. 3). Beyond

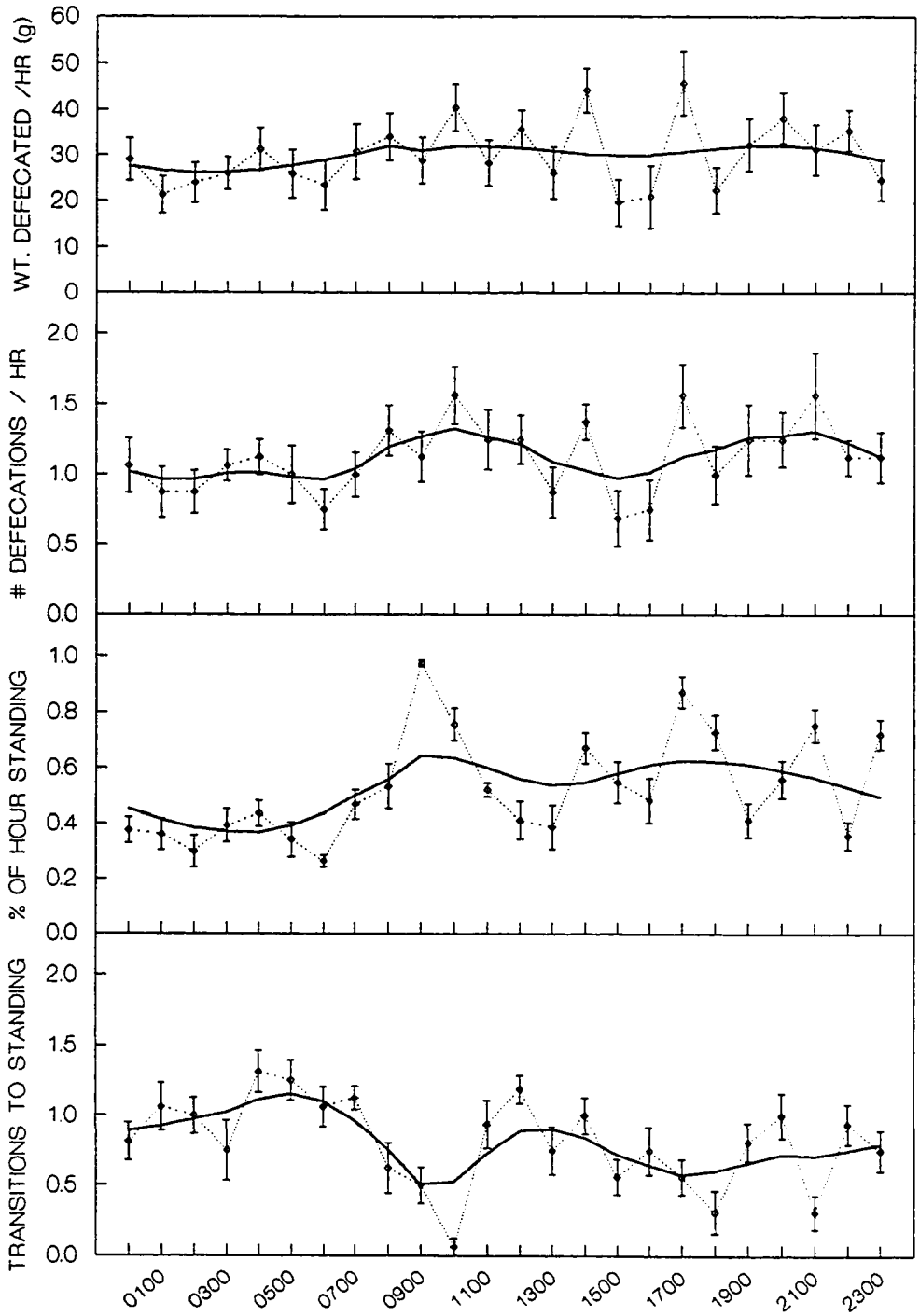

Fig. 2. Hourly excretion rate (g), defecation rate, percent of hour spent standing, and number of transitions to standing for 4 female domestic ewes averaged over 4 days (dotted line). Error bars are SE and solid line was derived by Lowess smoothing.

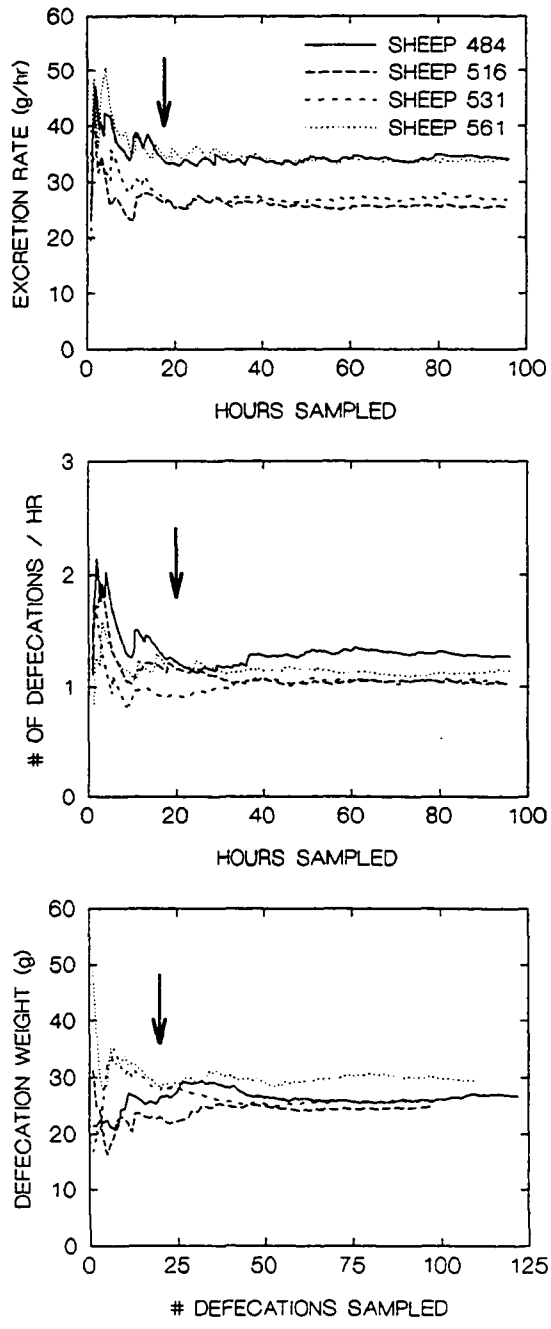

Fig. 3. Effect of number of hours sampled on mean excretion rate (g/hr) and defecation rate (# defecations/hr) and effect of number of defecations sampled on mean defecation weight (g/defecation) for 4 female domestic ewes averaged over 4 days.

this point of diminishing returns, additional hours of sampling yielded only slight improvements in the accuracy and precision of our estimates. We obtained similar results for the alternative sampling strategy of separately collecting information on number of defecations per hour and mean weight per defecation. Estimates of mean number of defecations per hour stabilized at 1.12 (SE = 0.06) after approximately 20 hours of sampling (Fig. 3). The effect of hour of day on weight of individual defecations was not significant ($F = 1.35$, $P = 0.126$), and so we used all defecations obtained for each ewe, in chronological order, to analyze estimated requirements for sample size and weight per defecation. Estimates of mean defecation weight stabilized at 26.8 g (SE = 1.00) after approximately 20 defecations (Fig. 3).

Dall's Sheep

A minimum of 5 samples was needed to stabilize estimates of mean weight per defecation for Dall's sheep ewes (Fig. 4). Mass per defecation in winter ($\bar{x}$ = 15.9 g, SE = 1.15, $n = 12$) was not different from mass per defecation during summer ($\bar{x}$ = 15.0 g, SE = 1.04, $n = 33$; $t = 0.458$, $P = 0.649$). Therefore, we combined these data, yielding a mean mass of 15.3 g/defecation (SE = 0.81, $n = 45$) throughout the year.

Estimates of number of defecations per hour for Dall's sheep ewes stabilized at approximately 20 hours (Fig. 4). Number of defecations per hour was higher in summer ($\bar{x}$ = 1.67, SE = 0.36, $n = 15$) than in winter ($\bar{x}$ = 0.69, SE = 0.18, $n = 13$; $t = 2.31$, $P = 0.029$). These estimates converted to a 24-hour basis yielded estimates of 40.0

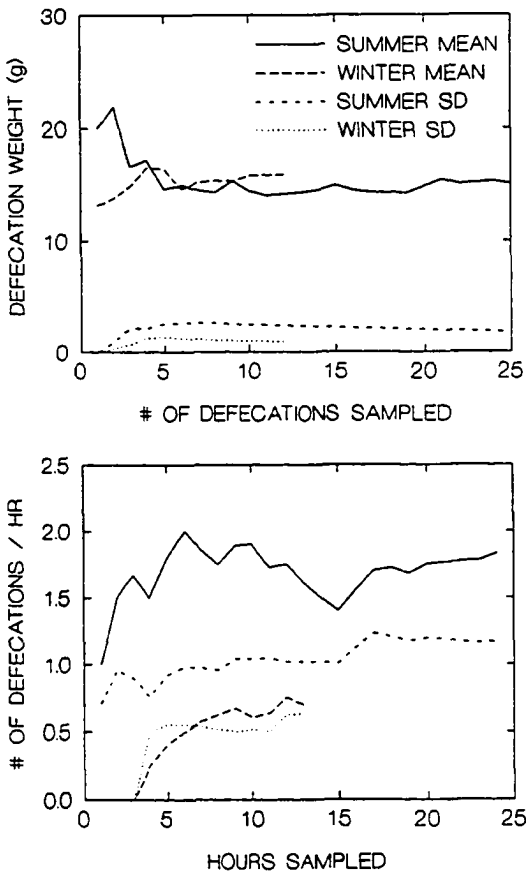

Fig. 4. Effect of number of defecations sampled on defecation weight (g/defecation) for free-ranging adult female Dall's sheep in the northern Brooks Range, Alaska from 1986 to 1988.

defecations/day and 612 g/day in summer versus 16.6 defecations/day and 254 g/day in winter (Table 5). Interpolation based on foraging time during 8 months suggests that free-ranging Dall's sheep ewes may have produced as few as 12.7 defecations/day in December and had excretion rates as low as 195 g/day (Fig. 5).

Mean mass of individual pellets became stable after sampling pellets from a minimum of 4 defecations from ewes and was estimated to average 0.20 g ($\underline{SE}$ = 0.01, $\underline{n}$ = 33) in summer and 0.22 g ($\underline{SE}$ = 0.01, $\underline{n}$ = 12) in winter. The seasonal estimates were not different ($\underline{U}$ = 103, $\underline{P}$ = 0.38), and the data were pooled to produce a mean mass of individual pellets of 0.20 g ($\underline{SE}$ = 0.01, $\underline{n}$ = 45) throughout the year. In late spring, however, unpelleted defecations occasionally were observed that probably resulted from the dietary shift to green forage.

DISCUSSION

Our data from domestic ewes on a combination of dry grass hay and pelleted alfalfa were consistent with the predictions of Blaxter et al. (1956), and ranged from 10 % above mean hourly excretion rates to 13 % below. The lowest excretion rates for our domestic ewes occurred during the early morning sampling period from 2300 to 0700 hours when most resting occurred; and highest excretion rates were measured from 0700 to 1300 hours, following this resting period. Excretion rates during the afternoon and evening sampling periods were near the mean. Therefore, when excretion rates are to be measured on an ungulate for which diurnal variation in behavior, and consequently in

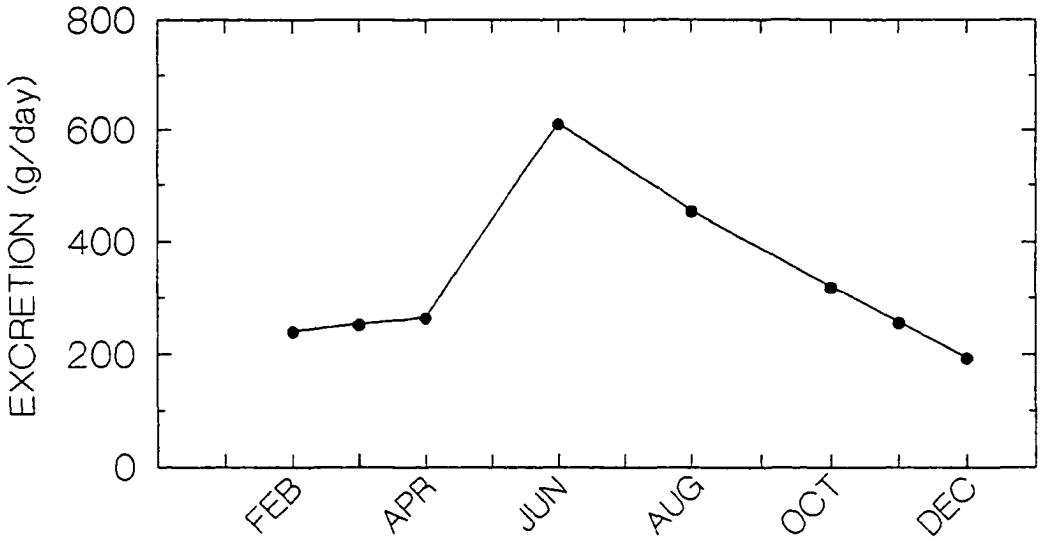

Fig. 5. Estimates of seasonal variation in daily excretion rate of free-ranging adult female Dall's sheep in the northern Brooks Range, Alaska from 1986 to 1988.

excretion rate, is expected, diurnal variation should be estimated. Where this is not possible, the diurnal variation may be measured on captive animals, and a correction applied to measures taken from wild animals or, alternatively, bias from diurnal variation can be minimized or avoided by not sampling during the primary rest period of the animals or the period immediately following the primary resting period.

For logistical reasons our sampling of free-ranging Dall's sheep ewes occurred entirely during the afternoon. Further, winter diets of Dall's sheep ewes consisted entirely of dried forage, largely sedges (55.5%) grasses (15.1%), and shrubs (11.4%) (Chapter 3). In similar diets for domestic sheep, there is little diurnal variation in excretion rate (Blaxter et al. 1956). In summer, ewes in the Brooks Range experienced no darkness and exhibited little activity of a diurnal pattern (Chapter 4), which should produce little diurnal variation in excretion rate. Consequently, we did not apply a correction for diurnal variation to our estimates of excretion rates of Dall's sheep ewes.

Marked differences in defecation rate have been associated with different behaviors. Church (1976:117) noted that most ruminants defecate after arising from a resting period, and our data from domestic sheep strongly support this view. Collins and Urness (1979) reported that elk defecated more often when traveling than during other behaviors. It may be that defecation by elk while traveling resulted from recently terminating a resting period, rather than as a result of the act of traveling. The defecations Collins and Urness (1979) noted simply may have been coincident with animal movement between bedding and foraging sites.

Most studies of defecation in wild ungulates have been associated with pellet-group indices of animal abundance. Defecation rates lower than we noted for Dall's sheep ewes in both winter and summer were reported for most penned ungulates, including several native North American and domestic species (Neff 1968), moose (Franzmann et al. 1976, Miquelle 1983), axis deer (Axis axis; Dinerstein and Dublin 1982), and several exotic species (Rollins et al. 1984). Studies of free-ranging white-tailed deer (Rogers 1987, Sawyer et al. 1990), however, reported defecation rates similar to those reported in this study. Higher defecation rates for free-ranging animals than for penned ones have been attributed to higher digestibility and availability of forage (Rogers 1987), but may also result from higher metabolic rates associated with greater levels of activity. Few studies have reported mass of defecations; in these, both mule deer (Arthur and Aldredge 1979) and white-tailed deer (McCullough 1982) produced larger defecations than we noted for Dall's sheep ewes, but mass of individual pellets was similar to mule deer (Arthur and Aldredge 1979).

Daily fecal excretion in winter by Dall's sheep ewes (254 g/day) was similar to that estimated for similar-sized white-tailed deer wintering in Michigan (297 g/day; McCullough 1982) and lower than mule deer in Colorado (396 g/day; Arthur and Aldredge 1980). Unfortunately, direct comparisons with these studies are difficult because both calculated excretion rates from defecation rates based on studies of penned animals. Direct comparisons are further limited because forage intake and, therefore, excretion is affected by body weight (Smith 1964), which was not reported.

Dall's sheep ewes we studied in summer exhibited daily rates of fecal excretion on a per kg body weight$^{0.75}$ basis similar to domestic ewes in our study, but lower than both penned mule deer (Dietz et al. 1962) and domestic sheep (Church 1976) fed alfalfa pellets only (Table 5). Domestic sheep fed a concentrate ration that was highly digestible (Church 1976), however, exhibited a low rate of fecal excretion similar to that we observed on poorly digestible winter diets of Dall's sheep. This likely resulted from lower intake from reduced appetite of sheep consuming such a highly digestibility diet (Van Soest 1982). Daily fecal excretion per kg body weight$^{0.75}$ of our Dall's sheep ewes in winter was similar to penned mule deer on simulated winter diets (Dietz et al. 1962). Excretion rates measured by Hebert (1973) for penned bighorn sheep on three diets with varying digestibility were lower than those we noted for both domestic ewes and Dall's sheep ewes in summer, however, the bighorn sheep in these experiments consumed about 1 kg of each forage type per day. With forage intake essentially constant, excretion rate was primarily affected by forage digestibility in Hebert's (1973) experiments.

In our study, intake of winter forage by Dall's sheep ewes likely was limited not only by digestibility, but also by environmental factors such as forage availability and snow cover. The low excretion rates we estimated for Dall's sheep ewes during winter probably resulted from a combination of both low digestibility and low intake of forage. Such low rates of excretion, in conjunction with the observation that ewes lost weight between October and March, indicate that these sheep consumed a sub-maintenance diet during much of the winter.

CONCLUSIONS

Although diurnal variation of excretion rate is affected by both forage digestibility and timing of forage intake, it is relatively consistent and predictable in Dall's sheep. Rates of excretion on shorter time scales, such as hourly, are much more variable, and are affected both by behaviors such as rising from a bed and by more instinctive mechanisms such as defecating when nervous or frightened (M. C. Hansen pers. obs.).

Observation periods <24 hours can provide estimates of daily fecal excretion for most ruminants consuming native forages. Species consuming highly digestible forages during a limited portion of the day may be an exception, and studies of these ungulates should assess the potential for bias from diel variation in foraging activity. Observation periods, whether continuous or random, should include both foraging and resting behavior, should not be biased toward continuous resting periods or the time immediately following such rest periods, and should incorporate analyses to insure adequate samples have been obtained.

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CHAPTER 3.

SEASONAL DIETARY COMPOSITION AND NUTRIENT INTAKE OF FREE-RANGING ADULT FEMALE DALL'S SHEEP[3]

ABSTRACT

We used microhistological analyses of fecal samples collected in the northcentral Brooks Range of Alaska between June 1986 and April 1988 to determine species composition of diets for free-ranging adult female Dall's sheep (ewes) (Ovis dalli dalli). We corrected diets to account for effects of differential digestibility. Nutrient analyses of both feces and simulated seasonal diets also were performed. Ewes primarily consumed forbs and grasses during summer. The bulk of their diets consisted of grasses in early winter with a gradual shift to sedges in February and back to grasses in early spring. Shrubs were consistently the least selected class of forage, largely because of their high abundance. Mosses and lichens were selected about in proportion to their availability. Forage quality was highest in June with mean total dietary nitrogen (TDN) levels of 3.1% (SD = 0.1) and lowest in December with mean TDN levels of 1.1% (SD = 0.1). Mean fecal nitrogen (FN) in June was 3.9% (SD = 0.4) and 1.9% (SD = 0.1) in December. In vitro dry matter digestibility (IVDMD) was measured at 63.0% (SD = 3.4) in June and

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[3] Prepared for publication as: Hansen, M. C., and D. R. Klein. 1996. Seasonal dietary composition and nutrient intake of free-ranging adult female Dall's sheep. J. Wildl. Manage. 00(0):000-000.

32.0% (SD = 6.1) in December. These estimates were probably low because apparent digestibility estimated by regression from FN was 81.5% (SD = 0.1) in June and 56.6% (SD = 3.7) in December. When the diet was composed of forages with varying digestibility, microhistological analyses of feces not corrected for differential digestibility were strongly biased toward less digestible forages. After correcting for digestibility, forbs were more important in summer diets of ewes than concluded by many previous studies. Winter forage available to ewes in the northern Brooks Range was highly limiting in both digestibility and protein content. Reduced daylight, and occasional snow cover on ridges usually wind-swept in winter, presumably further limited the ability of ewes to locate available forage. Consequently, winter weight losses of 30% were not uncommon for adult ewes.

INTRODUCTION

Dall's sheep (Ovis dalli and ancestors) apparently have been resident in the Brooks Range of Alaska for more than 125,000 years (Korobitsyna 1974), and have adapted to the extreme environmental conditions of the region. Nevertheless, extreme cold, darkness, and limited quantities of low-quality forage during long winters above the Arctic Circle present a formidable challenge for these large herbivores which are primarily diurnal. Further, summer is particularly short at these high latitudes, providing little time for sheep to accumulate energy reserves for winter. Despite these environmental factors, the Brooks Range contains large numbers of Dall's sheep, often at high densities

(Summerfield 1974, McDonald et al. 1990). To have persisted under such harsh environmental conditions over this time suggests that these ungulates should have developed foraging habits that optimize their use of the available resources (Pyke et al. 1977, Owen-Smith and Novellie 1982). A comprehensive study of foraging behavior and food habits of the closely related Stone sheep (O. d. stonei) in similar habitats in northern British Columbia, Canada (Seip and Bunnell 1985), however, concluded that forbs, the most nutritious and digestible forage in summer, were not selected -- an apparent deviation from optimal foraging theory.

Few studies of the foraging ecology of Dall's or Stone sheep exist that might confirm the nonoptimal foraging reported by Seip and Bunnell (1985), particularly near the northern extreme of the range of wild sheep in North America, where natural selection pressures might be expected to be strongest for optimal use of resources. Prior to this study, only 1 other has focused on foraging of Dall's sheep at similar latitudes (Ayres 1986). All other information on diets and foraging of Dall's sheep comes from more southern areas with longer periods of daylight during winter. Hoefs (1975) and Hoefs and Cowan (1979) included data on winter diets in their comprehensive study of Dall's sheep in Kluane National Park, Yukon Territory, Canada. In the Alaska Range, Whitten (1975) collected information on seasonal diets incidental to a study of habitat and population dynamics, and Elliott and McKendrick (1984) reported on winter and summer diets of Dall's sheep on a reclaimed strip-mined area. Also in the Alaska Range, Winters (1980) investigated summer habitat and food utilization, and Heimer (1983) investigated the

relationship between forage and "population quality." Other comparative data on foraging behavior and food habits are available for Stone sheep (Luckhurst 1973).

Of these studies, only Ayres (1986) calculated selection indices, but these were based on availability values measured at local feeding sites and did not address selection at other levels (Johnson 1980). Further, although most of these studies used microhistological analyses of rumen or feces, none corrected for differential digestibility of forages in determining diet composition. This study had 2 primary objectives: (1) to investigate forage selection of Dall's sheep near the northern extreme of their range and determine whether their foraging behavior indeed deviated from predictions of optimal foraging theory, and (2) to estimate energy and nitrogen intake on a seasonal basis, which could be used in modeling annual energy budgets of Dall's sheep to help land and wildlife managers anticipate effects of various management actions. Therefore, we tested the following specific null hypotheses: (1) sheep actively selected the forb forage class over other available forages in summer, (2) diet composition determined by microhistological analysis with correction for differential digestibility did not differ from uncorrected diet composition, (3) diet composition was not different among seasons or years, (4) diet composition did not differ between 2 portions of the study area, (5) presence of snow did not affect diet composition, (6) ewes consumed forage plants in proportion to plant species availability, (7) selection rankings for grasses and other graminoids did not change through winter as relative species availability changed, (8) FN was correlated with TDN,

digestible dietary nitrogen (DDN), and IVDMD for ewes, and (9) diet quality was not affected by season, year, portion of the study area, or presence of snow.

STUDY AREA

We conducted field work in the northern Brooks Range of Alaska (68.5° N, 149.3° W), primarily within the western edge of the Arctic National Wildlife Refuge. The area encompassed 2 portions: an intensive study area surrounding Black Mountain, which is adjacent to the Trans-Alaska Oil Pipeline (TAP) and associated Dalton Highway; and Atigun Gorge which extends to the northeast away from the pipeline and highway. Day length varied from 24 hours/day for about 60 days near the summer solstice, to no direct sunlight and only 3-4 hours of civil twilight daily for about 50 days near the winter solstice. Daily temperature averaged 10 C in July and -29 C in January. Elevation where we observed ewes ranged from 600 to 1,400 m.

Six vegetation types occur in the study area. In poorly drained soils and valley bottoms a sedge-rush vegetation type is dominated by Eriophorum vaginatum and several species of Carex. In deeper soils that were well drained, Betula nana and several species of Salix form a shrub-dominated vegetation type. On steeper slopes that ewes primarily inhabited, 3 low-growing types of tundra vegetation are interspersed with areas of rock, scree, and disturbed soil. Dryas octopetala dominates 1 of the tundra vegetation types and forms dense mats on slopes with stable soil and especially on northern exposures. On some south-facing slopes Kobresia myosuroides dominates another tundra vegetation

of several grasses and other graminoids. The third type of tundra vegetation occurs on fringes of disturbed soil on south-facing slopes and is dominated by Potentilla nivea and various mosses, but several grasses and forbs also are present. Most of the higher elevations are dominated by bare rock and scree. The sixth vegetation type occurred on gravel pads constructed to support the Trans Alaska Oil Pipeline (TAP) and on an adjacent gravel pit and primarily consisted of several nonnative grasses.

METHODS

Forage Availability

Vegetation Cover.--We partitioned the area used by ewes in the Black Mountain portion of the study area into 13 land blocks. Ridges and draws were used to delineate 4 blocks on northeast and northwest slopes ($\bar{x}$ = 47.0, SD = 31.4 ha), 3 blocks on south slopes ($\bar{x}$ = 44.1, SD = 29.5 ha), and 4 blocks on west slopes ($\bar{x}$ = 79.1, SD = 95.3 ha). Percent cover of each of Dryas, Potentilla, Kobresia, sedge, and shrub vegetation types, bare soil, and rock was determined on 1 block of each aspect during August 1987. We used a point sampling system similar to that used by Reynolds and Edwards (1977) to sample cover of smaller plots. The system involved using a Questar 120 power telescope and tripod located 0.5-1.5 km horizontally from the steep slope, we directed the telescope in a grid pattern to 200 points of each block in an approximation of systematic sampling (Cochran 1977). We initially held our eye slightly away from the eyepiece at each point it such that field of view included a small area of vegetation (approx 10 cm); then, by

moving the eye closer to the eyepiece and enlarging the field of view, it was possible to identify the vegetation type in which the point occurred. The telescope was then moved to the next point. We then calculated the proportion of the slopes of Black Mountain occupied by each type excluding nonvegetated ground. To this we added 1 large block of flatter, mostly sedge vegetation at the base of the mountain (300 ha), and another block that included 5.8 km of gravel pad supporting the TAP and a gravel pit that had been partially revegetated with non-native grasses (17.0 ha).

We used 6-8 circular plots (0.25 m^2) in each of the Dryas, Kobresia, and Potentilla types to visually estimate basal cover of individual plant species by vegetation type. A circular template delineating 1, 2, 5, and 10% of the plot was used to standardize visual estimates. Because the small circular plots were ineffective for measuring crown cover of shrubs (Gysel and Lyon 1980), we used the line intercept method (Canfield 1941) with 3, 50-m line transects in the shrub vegetation to estimate both crown cover of shrubs and basal cover of herbaceous plants. The revegetated and sedge vegetation were not initially considered habitat, and so were not sampled with plots or transects. Basal cover of these 2 vegetation types was subjectively estimated from photos and field notes following field work. Plots and transects for each type were spaced vertically up the slope and were measured in August 1987 at the end of the growing season and before most forbs were removed by grazing or covered by snow. Using these proportions and the area of each vegetation type, we estimated percent availability of each plant species on Black Mountain, and this was used in forage selection index calculations.

Seasonal Biomass.-- For most of the selection analyses, we assumed that basal cover of various forage plants did not change seasonally. Although basal cover of grasses and sedges may not change during the nongrowing period, we were concerned that preferential grazing by sheep might alter the relative weight of forage available from each forage species as the winter progressed, thus biasing selection indices. Therefore, we clipped 6-8 circular plots (0.25 m^2) in each of the Dryas, Kobresia, and Potentilla types to determine weight of forage available at the end of the growing season in August 1987. We then established a series of Michaelis-Menton equations (Real 1977, 1979):

$$\text{Weight} = \text{PercentBasalCover} \times \left(\frac{\text{MeanLength} \times P_1}{\text{MeanLength} + P_2} \right),$$

where P_1 is the asymptote of the curve and P_2 is related to the degree of curvature. The coefficients P_1 and P_2 for each plant species were derived from data on weight and length obtained by clipping individual plants progressively closer to the ground and weighing each clipped portion of the plant as described by Telfer (1969) for several species of browse. To estimate weight of forage plants remaining as winter progressed, we established and marked 5 sets of 15 plots (0.25 m^2) spaced vertically up the southwest slope of the mountain. We visually estimated basal cover of grazed and ungrazed portions of all grasses, sedges, and rushes in each of these plots in October, December, February, and April of the winter of 1987-88. Above-ground length of 10 leaves and 10 stems was measured for ungrazed portions of each plant species and, separately, of 10 leaves and 10 stems of grazed portions. We then estimated weight of each species remaining with nonlinear regression using the Michaelis-Menton equations.

Diet Composition

Bi-monthly (every other month) between April 1986 and April 1988 we located adult female Dall's sheep visually and collected entire, individual defecations. Occasionally feces were collected from areas where snow cratering or other sign indicated fecal material was <1 day old. Material that might have been mixed with older defecations was not collected. Samples were air-dried over a heater and stored in individual paper bags until analysis. All laboratory analyses were conducted at the Wildlife Habitat Laboratory, Washington State University, Pullman.

During the first year of field work, composite samples for June, August, October, December, February, and April were analyzed for forage composition to the species level by microhistological analysis of 300 microscope fields (Davitt and Nelson 1980). Each composite sample was constructed by combining 1 g of material from each of 15 fecal samples collected during the sample period (Anthony and Smith 1974). During the second year of field work, fecal samples were again collected during the same 6 months, and simultaneously we collected samples of forage plants that occurred in the diets during same sampling period of the previous year. Forage samples were collected by pinching the vegetation between thumb and the side of the curled forefinger to simulate the mouth size of sheep. Considerable effort was expended to select the most succulent, leafy plant material available in areas where ewes had recently been observed foraging. Following the second year of field work, 15 individual fecal samples from each of the 12 bi-monthly

sample periods were analyzed for forage composition to the species level. Each individual sample was analyzed separately with 20 microscope fields to make a total of 300 fields for each sample period.

During the first year of data collection, we noticed an apparent difference between diets of ewes living on Black Mountain, near the TAP, and those living in Atigun Gorge, about 8 km from the TAP. Consequently, during the latter part of the study we collected separate sets of fecal samples in these 2 areas. Additionally, on 2 occasions we had opportunity to collect separate sets of samples before and after a rapid change in snow cover on the study area. On 16 August 1986, near the end of summer, 13 fecal samples were collected. A sudden storm dropped 15 cm of snow on 21 August, and we collected 8 more samples on 24 August. On 2 December 1986, we collected 9 fecal samples from ewes feeding by cratering through 10 cm of crusted snow. That night a strong wind cleared nearly all snow off of south slopes, and on 6 December we collected 6 more fecal samples. These 8 sets of fecal samples also were analyzed for diet composition.

Correction factors for differential digestibility were calculated from the results of in vitro digestion of simulated diets assembled from forage samples (Dearden et al. 1975, Holechek and Valdez 1985) collected during each of the 6 bi-monthly sample periods in the second year of the study. Much of the forb forage class was not classified to genera, so we used material mixed from forbs identified in to genus as a substitute in assembling diets. Rumen inocula for this process were from domestic sheep maintained on grass hay.

Correction factors for differential digestibility from the second year of study then were used to adjust the diets estimated from fecal analyses for both years of the study.

All statistical comparisons, other than between Black Mountain and Atigun Gorge, were done on data from Black Mountain, with the exception of October 1986 and April 1987, when no samples were collected at Black Mountain and samples from Atigun Gorge were substituted. Most of these data on diets of ewes fit the assumptions of normality and uniformity of variances for parametric analyses, whereas other data were skewed by inclusion of several zero values. We used multivariate and univariate ANOVA for most statistical analyses (Neter and Wasserman 1974, Wilkinson 1990). The effect of the digestibility correction process was examined by comparing corrected and uncorrected diets using the 6 forage classes as dependent variables, whereas year, bi-monthly sample period, and sample number were used as independent blocking variables. The effects of season and year on corrected diets were tested by a 2-way multivariate ANOVA. For each forage class that showed significant changes, univariate ANOVA's and Bonferroni adjusted pairwise comparisons were also conducted (Wilkinson 1990). Seasonal variation in use of taxa within both forb and shrub forage classes was analyzed by the Kruskal-Wallis test because the inclusion of many zero values in these data violated assumptions of parametric analyses (Wilkinson 1990). For each taxa that showed significant changes, Mann-Whitney tests were performed with the Bonferroni adjustment for multiple comparisons (Wilkinson 1990). We used a general threshold level of significance of $\underline{\alpha} = 0.05$, and a family level of significance of $\underline{\alpha} = 0.05$ for multiple comparisons. The

same techniques were used to evaluate effects of snow cover and differences between portions of the study area.

Diet Selection

Our study design incorporated percent use of forage plants on an individual basis (15 pellet groups / period) and a single measure of percent availability of each plant species for the study area. Therefore, we used the Friedman method described by Alldredge and Ratti (1986) and Thomas and Taylor (1990), which incorporated a nonparametric overall test of similarity (Friedman) with a multiple comparisons test (Fischer's least significant difference [LSD]) when the Friedman test was significant. For illustrative purposes, we used box plots of percent use minus percent availability for each plant species or forage class.

Forage and Nutrient Intake

Simulated seasonal diets were constructed from the forage samples collected in the second year of the study based on corrected diet composition. Simulated diets were analyzed for Kjeldahl nitrogen (N), acid detergent fiber (ADF), acid detergent lignin (ADL) (Goering and Van Soest 1970), IVDMD (Tilley and Terry 1963), gross energy (GE) using bomb calorimetry, and total ash (ASH). Residue from the digestion process was then used as simulated fecal material, and was analyzed for GE, N, ADF, and ADL. Digestible nitrogen and energy were then calculated as the difference between the

simulated diets and the IVDMD residue. Metabolizable energy was calculated (Moe et al. 1972) as:

$$ME = (0.96 \times DE) - 1.13.$$

Calories (cal) were converted to Joules (J) by multiplying by 4.184 when necessary. Statistical comparisons among seasons were performed by ANOVA procedures.

Eight individual fecal samples from each of the 12 bi-monthly periods were analyzed for N and ASH. Five of the 8 samples from each of the 6 bi-monthly sample periods in the second year also were analyzed for ADF, ADL, and GE. In addition, 8 other sample periods representing comparisons between portions of the study area and comparisons between presence and absence of snow were similarly analyzed for N and ASH. Values presented for FN are expressed as percent of ash-free dry matter to eliminate extraneous variability (Wehausen 1995) resulting from ingestion of soil accidentally and at mineral licks (Young and Corbett 1972, Seip 1983:73) and from surface contamination (Howery and Pfister 1990). Statistical comparisons among seasons, years, portions of the study area, and snow conditions were performed by separate ANOVA procedures. Linear regression was used to examine the relationship between FN and TDN, DDN, and IVDMD. For these regressions IVDMD was natural log transformed (Wehausen 1995).

Four methods were used to calculate dry matter intake (DMI) from fecal excretion values estimated primarily from reproductive ewes in the field (Chapter 2). The first 2 methods used ADL and ADF in the simulated diets and associated fecal samples as

markers for ratio calculations. Because comparison of ADL and ADF before and after in vitro digestion showed that neither ADL nor ADF exhibited zero digestibility, we used digestibility rates from these trials to correct the ratio calculations of daily DMI:

$$DMI = \frac{\text{Fecal Excreion} \times \text{Marker in Forage}}{\left(\frac{1}{\text{Marker Digestibility}}\right) \times (\text{Marker in Feces})}.$$

The third method simply divided daily fecal excretion (Chapter 2) by IVDMD from the simulated diets. The IVDMD procedure involved an extended digestion period of 60 hours. Nevertheless, Milchunas et al. (1978) reported that digestibility of grasses after 48 hours was 85% of their final digestibility after 100 hours. Dry graminoids composed the bulk of diets for ewes during the 4 winter months and these forages are retained in the rumen longer than 48 hours (Milchunas et al. 1978). Therefore, we divided IVDMD rates during winter by 0.85 to account for the longer rumen residence time in intake calculations:

$$DMI = \frac{\text{Fecal Excretion}}{\left(\frac{1-\text{IVDMD}}{0.85}\right)}.$$

For the fourth method, we estimated apparent digestibility by regression from FN (Wehausen 1995) and used this alternative measure of digestibility to calculate DMI as:

$$DMI = \frac{\text{Fecal Excretion}}{(1 - \text{Apparent Digestibility})}.$$

Comparison with other studies was facilitated by dividing DMI by average body weight$^{0.75}$ as suggested by Blaxter et al. (1961) for domestic sheep. Average body weight of adult

ewes in our study was determined by weighing live-captured animals during October ($\bar{x}$ = 68.8, SD = 3.8 kg, n = 5) and March ($\bar{x}$ = 56.0, SD = 1.7 kg, n = 3).

RESULTS

Forage Availability

Vegetation Cover.--The sedge, Dryas, and shrub vegetation types together constituted 90% of the vegetated area available to sheep on Black Mountain (Table 6). Consequently, Eriophorum, Dryas, Salix, and Carex capillaris, the most common taxa in these vegetation types, dominated the available forage plants in the study area. Dryas, Kobresia, Potentilla, and shrub vegetation types were the primary types in the terrain ewes were observed to use. Sedge and revegetated types primarily occurred on flatter terrain surrounding the mountain and were used less frequently.

The Dryas type was dominated by Dryas and litter, but contained low densities of several plants from each of the forage classes (Table 6). The Kobresia type was dominated by the sedge Kobresia myosuroides and litter, but also contained a fairly high density of forbs, grasses, and other sedges. Potentilla sites were often on the periphery of scree slopes and usually on shallow soils. This vegetation type was dominated by Potentilla nivea, but contained many other forbs. The shrub vegetation type was dominated by Salix and other shrubs, including Betula nana and Vaccinium uliginosum.

Table 6. Percent composition of 6 vegetation types and weighted mean basal cover of herbaceous plants and crown cover of shrubs, excluding non-vegetated areas, for the entire Black Mountain study area in the northern Brooks Range, Alaska from 1986 to 1988.

	Vegetation type						Weighted[d]
Plant Taxa / Cover Type	Dryas[a]	Kobresia[a]	Potentilla[a]	Shrub[b]	Sedge[c]	Reveg.[c]	Mean
Area (km^2)	2.50	0.47	0.16	1.57	2.99	0.17	
Rock	0.3	0.5	12.4	1.0	0.0	15.0	0.9
Soil	0.0	3.4	21.9	0.2	5.0	70.0	4.1
Litter	58.5	52.3	23.4	6.2	40.0	2.0	38.8
Forbs							
Antennaria friesiana	0.0	0.0	0.1	0.0	0.0	0.0	0.0
Epilobium latifolium	0.0	1.1	0.2	0.0	0.0	0.3	0.1
Hedysarum mackenzii	0.0	0.5	0.0	0.0	0.0	0.0	0.0
Potentilla spp.	0.1	3.3	9.6	1.8	0.0	0.0	0.8
Saxifraga spp.	0.9	0.8	0.7	0.6	0.5	0.0	0.7
Other forbs	2.0	2.9	4.8	0.5	4.0	2.8	2.6
Subtotal	2.9	8.8	15.3	2.9	4.5	3.1	4.1
Grasses							
Agropyron macrorum	0.0	0.0	0.0	0.0	0.0	3.0	0.1
Arctagrostis latifolia	0.0	0.0	0.0	0.0	1.0	1.0	0.4
Bromus pumpellianus	0.0	1.1	0.4	0.1	0.0	0.0	0.1
Festuca spp.	0.3	0.1	0.0	1.9	0.0	3.0	0.6
Poa spp.	0.4	1.8	1.4	0.0	0.0	3.0	0.3
Other grasses	0.6	0.5	0.8	0.2	2.0	0.0	1.0
Subtotal	1.3	3.6	2.6	2.2	3.0	10.0	2.5
Sedges/Rushes							
Carex bigelowii	0.3	2.0	0.0	0.1	0.0	0.0	0.2
Carex capilaris	0.0	0.0	0.0	0.0	12.0	0.0	4.6
Carex rupestris	0.6	3.1	2.5	0.1	0.0	0.0	0.5
Eriophorum spp.	0.0	0.0	0.0	0.0	27.5	0.0	10.5
Kobresia myosuroides	0.5	9.7	0.0	0.5	0.0	0.0	0.8
Luzula tundricola	0.0	0.0	0.0	0.0	0.5	0.0	0.2
Subtotal	1.4	14.9	2.6	0.7	40.0	0.0	17.7
Shrubs							
Dryas spp.	29.3	1.2	0.0	0.1	0.0	0.0	9.4
Salix spp.	0.7	0.3	0.0	45.7	0.0	0.0	9.4
Vaccinium uliginosum	0.0	0.0	0.0	9.6	0.0	0.0	1.9
Other shrubs	1.2	1.5	0.4	26.7	0.0	0.0	5.8
Subtotal	31.2	2.9	0.4	82.2	0.0	0.0	26.6
Lichen	0.6	2.5	5.5	0.5	2.5	0.0	1.5
Moss	3.2	10.7	15.4	4.5	5.0	0.0	4.7

[a] Proportions estimated from 0.25 m^2 plots.
[b] Proportions estimated from 25 m line transects.
[c] Proportions estimated from photos and notes.
[d] Mean cover of plant taxa across plant vegetation types weighted by area (km2) of each vegetation type in the study area.

The sedge vegetation type was dominated by Eriophorum and several species of Carex, but also contained several forbs and grasses.

Seasonal Biomass.--On the Kobresia tundra vegetation type, seasonal weight of forage available declined in only 3 of the 7 forage species measured. Weight of Poa glauca dropped steadily from August ($\bar{x}$ = 1.7 g/m^2) to April ($\bar{x}$ = 0.4 g/m^2, U = 436, P = 0.003). Weight of Kobresia myosuroides declined abruptly from October ($\bar{x}$ = 19.6 g/m^2) to December ($\bar{x}$ = 7.6 g/m^2, U = 2978, P < 0.001). Weight of Carex rupestris did not begin dropping until December ($\bar{x}$ = 4.4 g/m^2), and by April averaged only 2.5 g/m^2 (U = 2312, P < 0.001). Carex bigelowii, Bromus pumpellianus, Trisetum spicatum, and Hierochloe alpina occurred infrequently in small amounts in this vegetation type and showed little or no change in weight through winter.

Diet Composition

Digestibility Corrections.--Although the digestibility correction process affected estimates of the relative proportion of forages in ewe diets during all seasons of the year, the greatest effects occurred in summer (Fig. 6). The proportion of forbs in uncorrected estimates of diet composition was much lower than in corrected estimates of diet composition (P < 0.001) during all periods of the year except December (F = 0.463, P = 0.500) and February (F = 2.355, P = 0.132). The correction process had less effect on grasses and lichens, although there were still significant differences in all months except October and February for grass and December, June, and April for lichen. Mosses were

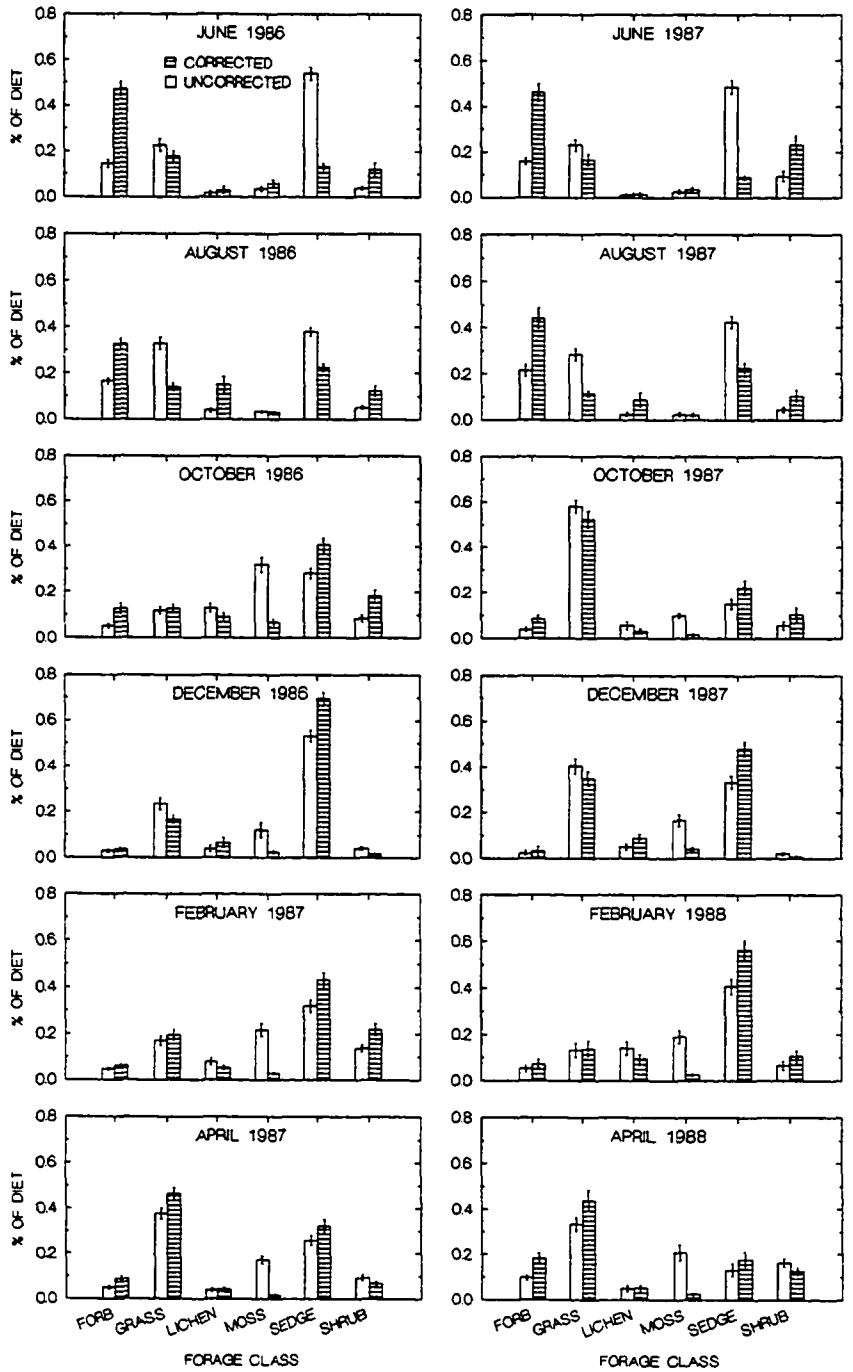

Fig. 6. Percent composition by forage class of free-ranging adult female Dall's sheep diets as determined by microhistological analyses before and after correction for differential digestibility in the northern Brooks Range, Alaska, 1986-1988.

highly over-represented in uncorrected estimates of diet composition ($P < 0.001$) in all months except August ($F = 0.214$, $P = 0.646$). Sedges and rushes were much lower in corrected diets than uncorrected estimates of diet composition in June ($F = 887.663$, $P < 0.001$) and August ($F = 138.052$, $P < 0.001$), slightly higher in the winter months ($P < 0.001$), and not different in April ($F = 3.973$, $P = 0.053$). Shrubs were generally higher in corrected diets than uncorrected estimates of diet composition ($P < 0.001$), but lower in December ($F = 13.633$, $P = 0.001$) and April ($F = 10.235$, $P = 0.003$).

Season Effects.--Corrected diet composition was strongly affected by month (Wilks' Lambda = 0.056, $P < 0.001$). The greatest seasonal changes in diet composition were in the proportion of forb ($F = 101.82$, $R^2 = 0.762$, $P < 0.001$), sedge/rush ($F = 73.65$, $R^2 = 0.726$, $P < 0.001$), and grass ($F = 38.58$, $R^2 = 0.659$, $P < 0.001$) forage classes (Fig. 7). Smaller changes were evident in shrubs ($F = 10.85$, $R^2 = 0.329$, $P < 0.001$) and lichens ($F = 5.55$, $R^2 = 0.192$, $P < 0.001$), although moss ($F = 2.89$, $R^2 = 0.207$, $P = 0.016$) changed the least.

Forbs were the primary forage class used in summer (Fig. 7), and were used more in June than in any other month ($\bar{x} = 46\%$, $P < 0.024$). They were used little during winter, especially during December ($\bar{x} = 4\%$). Within the forb forage class, ewes used a large number of taxa during all seasons of the year, but most taxa were used only in small amounts (Fig. 8). Four genera were used in greater than trace amounts. Antennaria was used in June and August more than during the remainder of the year ($U > 630$, $P < 0.001$). Epilobium was used more in June than during the remainder of the year

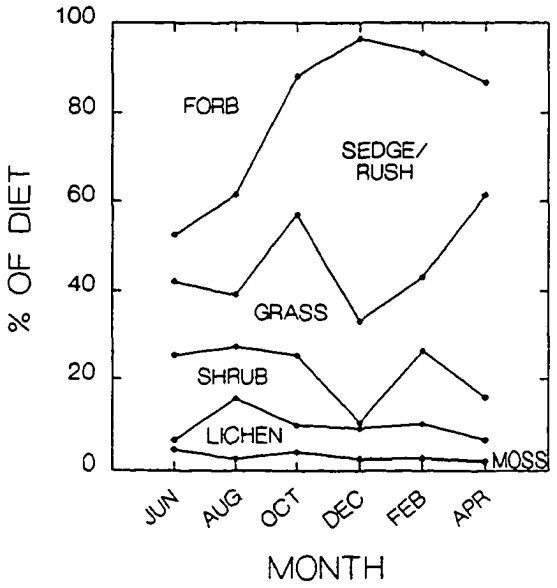

Fig. 7. Average cumulative percent composition by forage class of free-ranging adult female Dall's sheep diets in the northern Brooks Range, Alaska, 1986-1988 after correction for differential digestibility.

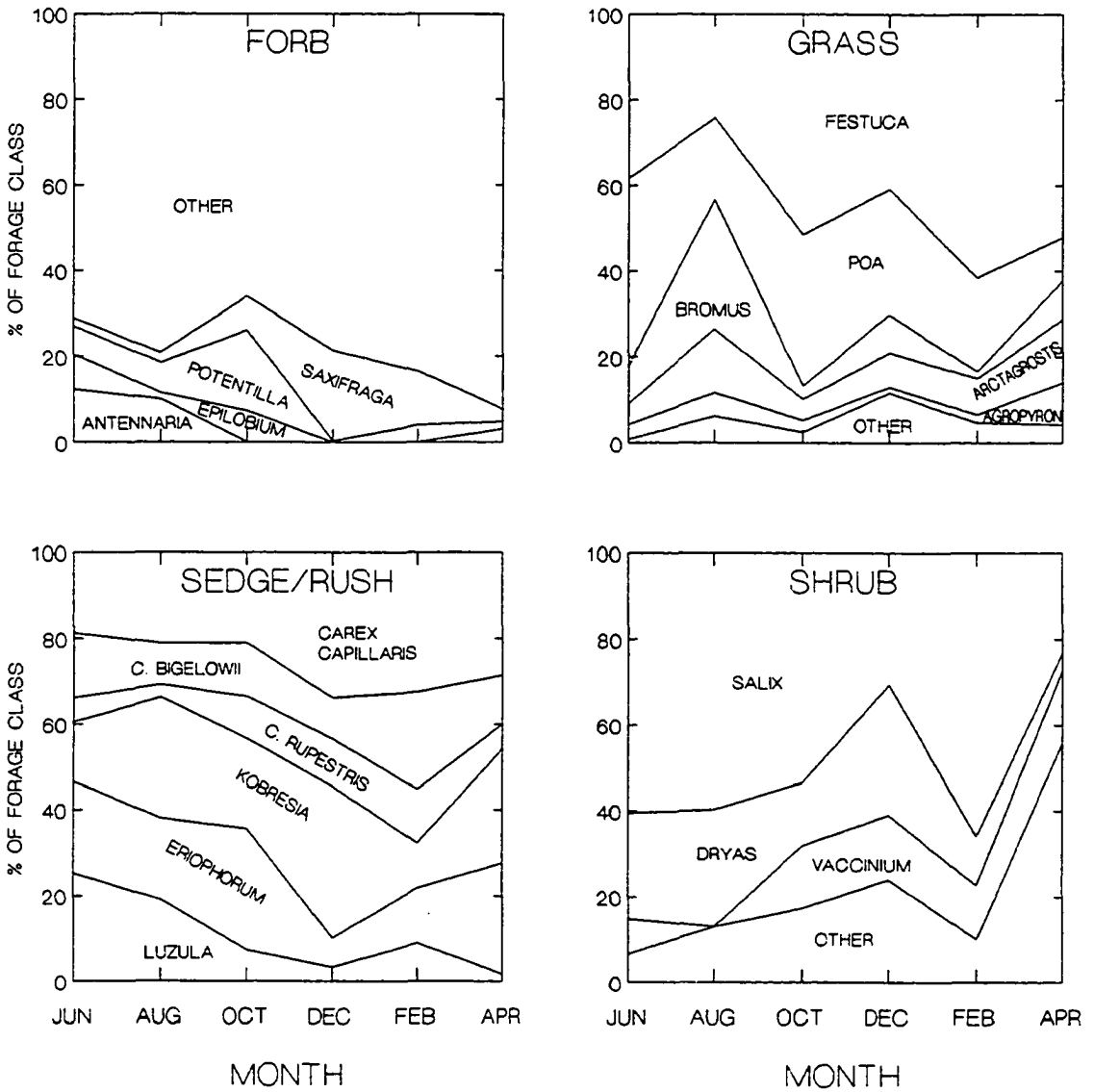

Fig. 8. Average cumulative percent composition by taxa of forb, grass, sedge/rush, and shrub forage classes in the diets of free-ranging adult female Dall's sheep in the northern Brooks Range, Alaska from 1986-1988 after correction for differential digestibility.

($U > 535$, $P < 0.011$). Potentilla, Saxifraga, and the other forb category were used throughout the year with no difference among bi-monthly sampling periods ($KW < 9.35$, $P > 0.096$).

Sedges and rushes were the primary forage class used in December ($\bar{x} = 58\%$) and February ($\bar{x} = 50\%$) (Fig. 7). They were used more during these months than during the remainder of the year ($P < 0.001$). Even during June, however, when they were used less than during the rest of the year ($\bar{x} = 11\%$, $P < 0.003$), sedges were still a substantial part of the diets. Within the sedge/rush forage class, 6 taxa were represented (Fig. 8). Carex capillaris made up more of the sedge/rush class in December than in June ($P < 0.039$). Both C. bigelowii and C. rupestris constituted slightly more of the sedge/rush class in February than during August ($P < 0.035$). Kobresia myosuroides made up slightly more of the sedge/rush class in December and less in February than during the remainder of the year ($P < 0.022$). Eriophorum constituted less of the sedge/rush forage class in December than in October ($P < 0.020$). Luzula tundricola made up more of the sedge/rush class in June and August than during the remainder of the year ($P < 0.026$).

Grasses were used most in April ($\bar{x} = 45\%$, $P < 0.001$), but were also consumed in greater amounts in October ($\bar{x} = 32\%$, $P < 0.001$) and December ($\bar{x} = 26\%$, $P < 0.035$) than during February or summer (Fig. 7). Agropyron macrourum was more common in the grass forage class in April than during the remainder of the winter ($P < 0.008$) (Fig. 8). Bromus pumpellianus made up more of the grass forage class in August than during the remainder of the year ($P < 0.001$). Festuca constituted less of the grass forage class in

August than during October, February, and April ($P < 0.033$). Poa composed less of the grass forage class in April than during June, October, and December ($P < 0.019$), and more of the grass forage class in June than during August, February, and April ($P < 0.013$). The other grass category made up more of the grass forage class in December than during June ($P < 0.019$).

Shrub use ranged from 10 to 18%, except during December when it was lowest ($\bar{x} = 2\%$, $P < 0.016$) (Fig. 7). Within the shrub class, Dryas was the only taxon that did not vary among months ($KW < 2.93$, $P = 0.711$) (Fig. 8). Salix was used less in December and April than in June and February ($U > 253$, $P < 0.012$). Both Vaccinium uliginosum and the "other shrub" category were used more in April than in any other month ($U > 140$, $P < 0.015$).

The proportion of lichens in the diets was relatively stable, with the only significant differences being between August ($\bar{x} = 12\%$) and both April ($\bar{x} = 5\%$) and June ($\bar{x} = 3\%$, $P < 0.005$). Similarly, moss composed a small proportion of the diets, and showed only a marginal difference between April ($\bar{x} = 3\%$) and June ($\bar{x} = 5\%$; $P = 0.057$).

Year Effects.--Overall, diet composition was different between years (Wilks' Lambda = 0.815, $P < 0.001$). Further, there was an interaction between sampling period and year (Wilks' Lambda = 0.380, $P < 0.001$) for all forage classes ($F > 2.42$, $P < 0.038$). There were changes in diet composition between years only for grass ($F = 22.54$, $P < 0.001$), sedge/rush ($F = 19.64$, $P < 0.001$), and moss ($F = 5.62$, $P = 0.019$) (Fig. 6).

No annual differences were evident in forbs ($F = 3.61$, $P = 0.059$), shrubs ($F = 0.25$, $P = 0.620$), and lichens ($F = 0.77$, $P = 0.382$).

Grasses, primarily Festuca and Poa, were used much more in October ($\bar{x} = 53\%$) and December ($\bar{x} = 35\%$) of 1987 than during October ($\bar{x} = 12\%$, $P < 0.001$) and December ($\bar{x} = 16\%$, $P < 0.035$) of 1986. Conversely, use of sedges, particularly Carex capillaris and Kobresia myosuroides (Table 7), was higher in 1986 than in 1987 during October ($P < 0.001$), December ($P < 0.001$), February ($P = 0.016$), and April ($P = 0.006$). Mosses also were used more in October 1986 ($\bar{x} = 7\%$) than in October 1987 ($\bar{x} = 2\%$, $P < 0.001$).

Area Effects.-- Overall composition of diets of ewes was slightly different between the 2 portions of the study area (Wilks' Lambda = 0.910, $P = 0.034$). Use of shrubs averaged 34.5% lower in the Black Mountain area than in the Atigun Gorge area ($F = 9.85$, $P = 0.002$), although forb use averaged 23.1% higher in the Black Mountain area ($F = 4.33$, $P = 0.039$). Although several shrubs were consumed less by ewes on Black Mountain, only for Salix during October ($U = 115$, $P = 0.026$) and December ($U = 161$, $P = 0.029$) were the differences significant. Among the forbs, significant differences occurred only for Saxifraga in October ($U = 37.5$, $P = 0.003$), which was used more in the Black Mountain area ($\bar{x} = 2.3\%$) than in Atigun Gorge ($\bar{x} = 0.0\%$). Additionally, a significant interaction between bi-monthly sampling period and area (Wilks' Lambda = 0.431, $P < 0.001$) for grass ($F = 14.50$, $P < 0.001$), lichen ($F = 13.65$,

Table 7. Percent diet composition (SD) corrected for digestibility and relative availability of food items making up ≥ 1% of bi-monthly diets for free-ranging adult female Dall's sheep in the northern Brooks Range, Alaska 1986-1988.

	Diet Composition												
	1986-87						1987-88						Relative
Food Item	Jun	Aug	Oct	Dec	Feb	Apr	Jun	Aug	Oct	Dec	Feb	Apr	Availability
No. of single samples	15	13	15	15	15	15	15	15	15	15	15	15	
Forbs													
Antennaria friesiana	5 (9)	4 (4)					6 (6)	3 (5)					tr
Epilobium latifolium	2 (5)		2 (6)				4 (6)	1 (3)				1 (4)	0.1
Hedysarum mackenzii							1 (3)	6 (4)					0.1
Potentilla spp.	3 (6)	tr	2 (4)	tr	1 (1)	tr	2 (4)	4 (8)	2 (5)	tr			1.4
Saxifraga spp.	1 (4)				1 (2)	1 (2)		1 (4)	1 (3)	tr	tr		1.2
Other	36 (13)	29 (10)	9 (8)	3 (3)	4 (3)	7 (5)	33 (14)	29 (12)	6 (5)	1 (1)	7 (7)	17 (10)	4.6
Subtotal	47 (13)	33 (8)	13 (10)	4 (3)	6 (3)	9 (5)	46 (14)	44 (18)	9 (7)	3 (7)	7 (8)	18 (9)	7.4
Grasses													
Agropyron macrourum	1 (2)	1 (2)	tr	tr	1 (1)	8 (8)	tr	1 (1)	2 (3)	tr	tr	1 (4)	0.1
Arctagrostis latifolia	1 (1)	2 (2)	tr	2 (2)	2 (2)	5 (5)	1 (1)	1 (2)	2 (2)	2 (3)	1 (2)	8 (11)	0.7
Bromus pumpellianus	2 (3)	5 (4)		2 (2)		3 (4)	1 (1)	2 (2)	2 (1)	3 (3)	1 (1)	4 (6)	0.2
Festuca spp.	6 (4)	2 (1)	8 (6)	4 (4)	14 (9)	23 (9)	7 (3)	4 (2)	26 (8)	18 (10)	6 (8)	25 (11)	1.0
Poa spp.	7 (5)	3 (2)	4 (4)	5 (4)	2 (3)	6 (3)	8 (7)	2 (1)	19 (8)	10 (5)	5 (8)	4 (3)	0.6
Other	tr	1 (1)	tr	3 (3)	1 (1)	1 (4)	tr	2 (3)	2 (2)	2 (3)	1 (1)	2 (4)	1.8
Subtotal	18 (9)	14 (7)	12 (7)	16 (7)	20 (9)	46 (10)	17 (10)	12 (5)	53 (14)	35 (12)	14 (14)	44 (18)	4.4
Sedges/Rushes													
Carex bigelowii	2 (1)	1 (1)	5 (2)	6 (4)	10 (5)	3 (3)	2 (1)	23 (1)	3 (4)	5 (4)	13 (10)	3 (2)	0.4
Carex capillaris	2 (1)	5 (3)	12 (7)	21 (8)	10 (5)	13 (8)	2 (1)	5 (3)	2 (2)	17 (8)	22 (12)	2 (3)	8.1
Carex rupestris	1 (1)	tr	5 (4)	8 (7)	5 (4)	2 (2)	tr	1 (1)	2 (3)	4 (4)	7 (9)	1 (2)	0.8
Eriophorum spp.	2 (2)	5 (6)	8 (6)	4 (3)	10 (9)	4 (7)	3 (2)	3 (3)	9 (13)	5 (4)	3 (5)	7 (14)	18.6
Kobresia myosuroides	1 (1)	6 (7)	10 (6)	27 (14)	4 (1)	10 (4)	2 (1)	6 (6)	2 (2)	15 (10)	7 (6)	3 (6)	1.5
Luzula tundricola	5 (3)	5 (5)	1 (3)	2 (2)	4 (3)		tr	4 (4)	4 (5)	2 (3)	4 (6)	1 (2)	0.4
Subtotal	13 (6)	22 (6)	41 (12)	69 (11)	43 (13)	32 (11)	9 (4)	23 (8)	22 (13)	48 (13)	56 (6)	17 (15)	31.5
Shrubs													
Dryas spp.	3 (9)	3 (4)	2 (3)	tr	2 (4)	1 (1)	6 (9)	3 (5)	2 (5)	tr	1 (5)	tr	16.8
Salix spp.	7 (8)	7 (9)	12 (10)	tr	14 (6)	4 (4)	14 (9)	7 (9)	4 (7)	tr	8 (10)		16.7
Vaccinium uliginosum			1 (3)	tr	3 (6)	1 (1)	2 (4)		3 (8)	tr	1 (3)	2 (2)	3.4
Other	2 (4)	3 (3)	3 (6)	tr	3 (4)	tr	tr		2 (3)	tr	1 (1)	11 (6)	10.4
Subtotal	12 (12)	13 (8)	18 (11)	3 (1)	22 (10)	7 (4)	23 (17)	10 (10)	11 (12)	1 (1)	11 (11)	13 (7)	47.3
Lichen	4 (7)	15 (13)	9 (7)	6 (9)	6 (4)	4 (3)	2 (2)	9 (12)	3 (4)	9 (8)	10 (8)	5 (5)	2.6
Moss	6 (6)	3 (2)	7 (4)	2 (3)	3 (2)	2 (1)	3 (5)	2 (3)	2 (1)	4 (3)	3 (2)	3 (2)	8.5

$P < 0.001$), sedge ($F = 5.40$, $P < 0.001$), and moss ($F = 3.95$, $P = 0.004$) resulted from inconsistent differences in use of these forage classes in the 2 portions of the study area among bi-monthly sample periods. Of these 4 forage classes, only grass showed differences that were consistent with seasonal patterns: they were more common in diets in the Black Mountain area during October, December, and February, but less common in April and June.

Snow Effects.--The snow storm in August 1986 affected the overall diets of ewes (Wilks' Lambda = 0.227, $P = 0.001$) (Fig. 9). After the snow storm, ewes ate less moss ($F = 16.63$, $P = 0.001$), less lichen ($F = 10.94$, $P = 0.004$), more shrubs ($F = 7.72$, $P = 0.012$), especially Dryas ($F = 14.97$, $P = 0.001$), and marginally less of the sedge and forage class rush ($F = 4.68$, $P = 0.044$). The removal of snow by wind in December had no effect on diet composition (Wilks' Lambda = 0.422, $P = 0.211$).

Diet Selection

Season Effects.--Ewes exhibited strong forage selection during both years and all seasons (Friedman > 39.8, $P < 0.001$). Forbs exhibited 1 of the largest seasonal changes in selection (Fig. 10). Forbs were the most highly selected class in June ($P < 0.001$) and August ($P < 0.008$), but were used in about the same proportion as their availability in winter. With the exception of forbs in summer, grasses were generally selected more than all other forage classes (Fig. 10). Grasses were selected most in early and late winter, and selected at similar rates to sedges in mid-winter. When strong selection was

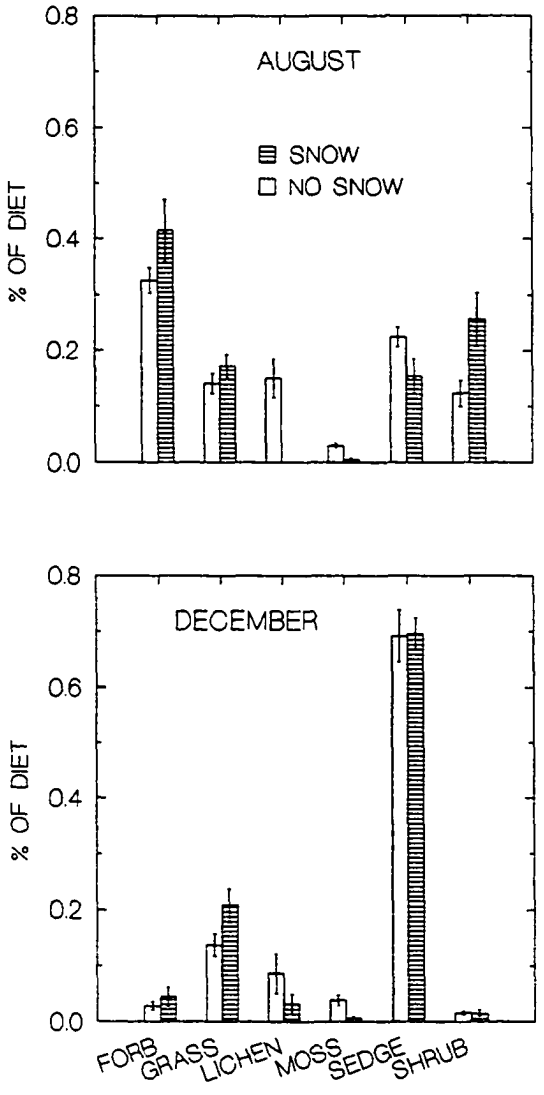

Fig. 9. Corrected percent composition by forage class of free-ranging adult female Dall's sheep diets in the presence and absence of 10-15 cm of uniform snow cover in the northern Brooks Range, Alaska in August and December 1986.

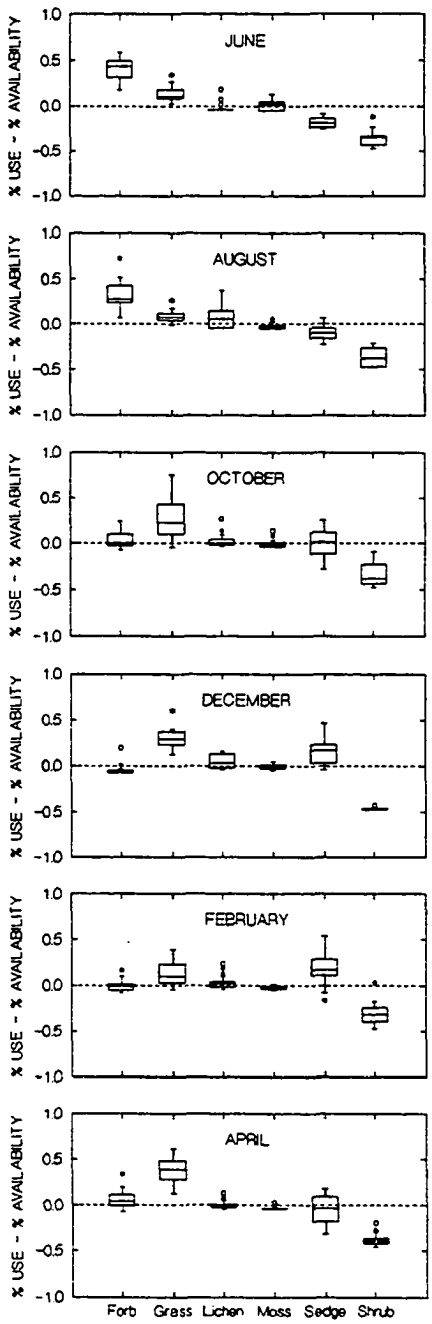

Fig. 10. Selection of free-ranging adult female Dall's sheep for forage classes in the northern Brooks Range, Alaska averaged bi-monthly over 2 years from 1986-1988.

shown among grasses, Festuca or Poa were the selected taxa (Fig. 11). Sedges and rushes were selected less than all other forage classes except shrubs in June ($P < 0.001$), but increased in selection until mid-winter when they were occasionally the most selected forage class. Among the sedges and rushes, Kobresia myosuroides and Luzula tundricola were generally the most selected in summer, although K. myosuroides and C. bigelowii were generally most selected in winter (Fig. 11). Eriophorum was consistently the least selected graminoid throughout the year. Carex capillaris also was selected less than other sedges, but in February 1988 was selected over all other sedges ($P < 0.042$) except C. bigelowii ($P = 0.882$). Lichens were used about in proportion to their availability most of the year, and slightly more than their availability during some winter months (Fig. 11). Mosses were consistently used less than their availability throughout the year. Shrubs were consistently the least selected forage class all year ($P < 0.001$) with the exception of June 1986 when the low selection for shrubs and sedges were not different ($P = 0.116$).

When selection was recalculated on the basis of weight of forage remaining for the 5 primary graminoids on the Kobresia vegetation type, the relative ranking among taxa did not differ from the rankings based on basal cover alone.

Year Effects.-- Between the 2 years there was little difference in relative selection among either forage classes or graminoid taxa in summer. The same was true for most of the winter months with the exception of October (Fig. 12). In October 1986, grasses and sedges ranked similarly ($P = 0.453$) whereas in October 1987 grasses,

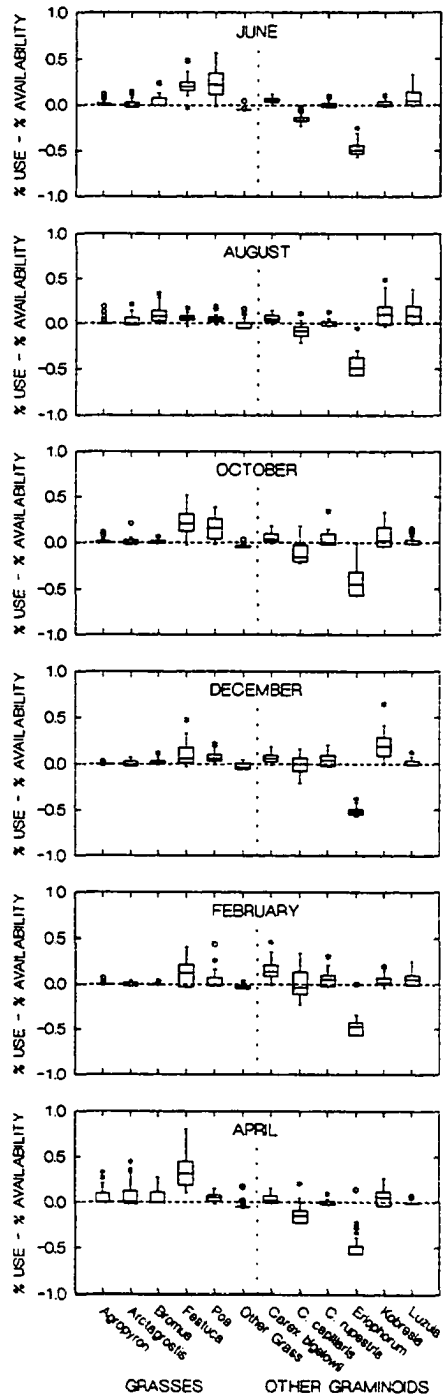

Fig. 11. Selection of free-ranging adult female Dall's sheep for taxa within the grass and sedge/rush forage classes in the northern Brooks Range, Alaska averaged bi-monthly over 2 years from 1986-1988.

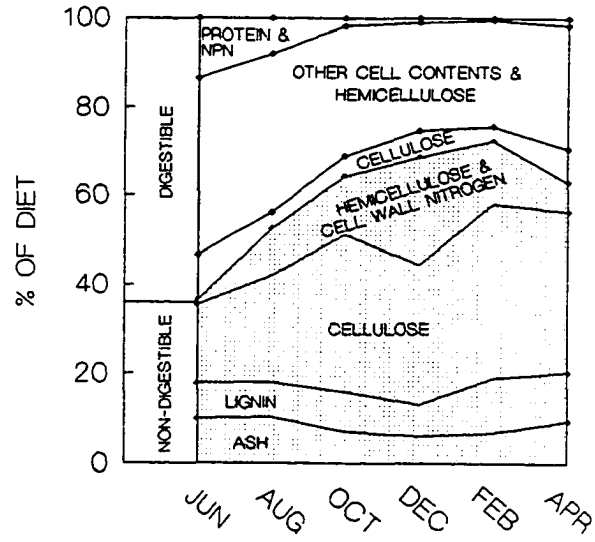

Fig. 12. Nutrient composition of free-ranging adult female Dall's sheep diets in the northern Brooks Range, Alaska averaged bi-monthly over 2 years from 1986-1988.

particularly Festuca and Poa, ranked much higher than sedges and all other forage classes ($P < 0.001$).

Diet Quality

Forage Measures.--Both forage digestibility and protein were highest in June and lowest in February (Fig. 12). Conversely, lignin and indigestible cellulose were lowest in June and highest in February. Indigestible hemicellulose and cell wall constituents followed a pattern similar to cellulose, except that they were at their highest levels in December (Fig. 12).

Nutrient content of the diet was affected by season (Wilk's Lambda = 0.001, $P < 0.001$). Month was highly correlated with IVDMD ($R^2 = 0.905$, $P = 0.005$), digestible energy (DE) ($R^2 = 0.930$, $P = 0.002$), DDN ($R^2 = 0.985$, $P < 0.001$), and ash ($R^2 = 0.905$, $P = 0.005$). IVDMD and DE were both higher during June than during all months except August ($P < 0.036$) (Fig. 13). Total digestible nitrogen was highest during June, and both June and August were different from all other months including each other ($P < 0.008$). Total ash was lower in December ($\bar{x} = 5.7\%$, $SD = 0.8$) than in June ($\bar{x} = 9.6\%$, $SD = 0.9$, $P = 0.025$) or August ($\bar{x} = 9.6\%$, $SD = 0.8$, $P = 0.025$), but no other differences occurred among months.

Although we did not test for differences between years or snow conditions because only 1 diet was analyzed for each year and snow condition, IVDMD and DE both appeared to be lower in 1987-88 than 1986-87 for all months except April (Fig. 13).

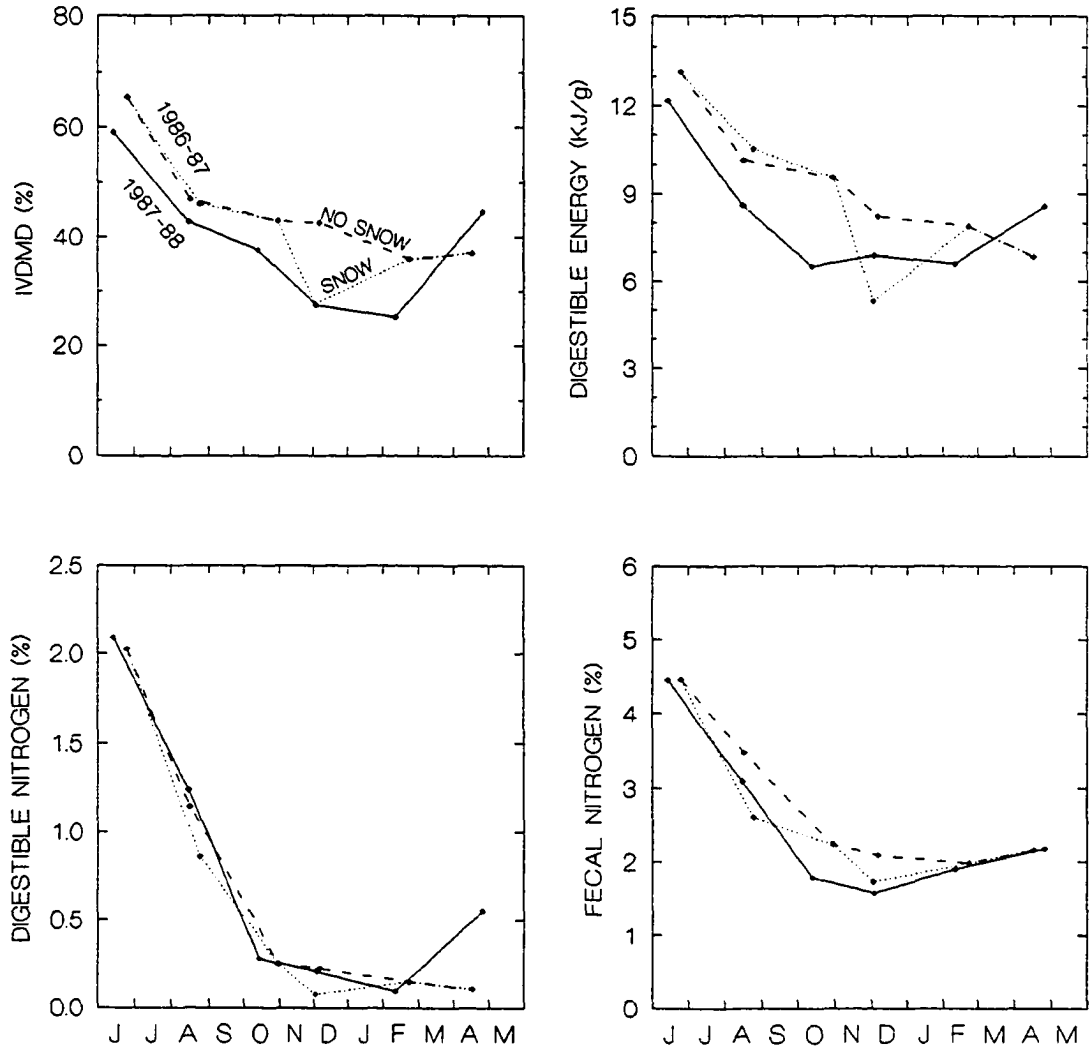

Fig. 13. Bi-monthly in vitro dry matter digestibility (IVDMD), digestible energy, and digestible protein in the diet and of fecal nitrogen for free-ranging adult female Dall's sheep in the northern Brooks Range, Alaska, 1986-1988.

IVDMD and DE also appeared to be much lower when snow was present in December than when ewes had access to wind-blown ridges (Fig. 13). Total digestible nitrogen varied little between 1986-87 and 1987-88 for most months, but appeared higher in April 1988 than in April 1987. Total digestible nitrogen also appeared to be lower when snow was present than when it was not for both the August and December storms (Fig. 13).

Fecal Nitrogen.--Like forage nitrogen, FN was strongly correlated with season (ANOVA, $F = 245.3$, $R^2 = 0.927$, $P < 0.001$). Fecal nitrogen was higher in June than in all other months ($P < 0.001$) (Fig. 13), and it was higher in August than October, December, February, or April ($P < 0.001$). Among the remaining months, only April and December were different ($P < 0.001$). Fecal nitrogen was higher in 1986-87 than in 1987-88 for August ($F = 10.71$, $P = 0.002$), October ($F = 14.26$, $P < 0.001$), and December ($F = 12.24$, $P = 0.001$), but not different for the remainder of the year ($F < 0.33$, $P > 0.565$).

When the 3 months for which we had comparable data from both the Black Mountain and Atigun Gorge were analyzed alone the effect of bi-monthly sample period was still significant ($F = 68.7$, $P < 0.001$), but no significant effect of study area on fecal nitrogen occurred ($F = 2.70$, $P = 0.106$). Similarly, using only 2 sets of data from before and after snow events, we noted significant effects of both month (ANOVA, $F = 162.6$, $P < 0.001$) and presence of snow ($F = 48.23$, $P < 0.001$). In this instance, FN was lower when snow was present ($\bar{x} = 2.61\%$, $SD = 0.25$, $n = 8$) than when it was absent ($\bar{x} = 3.48\%$, $SD = 0.37$, $n = 8$) during August ($F = 31.66$, $P < 0.001$), as well as when

snow was present ($\bar{x}$ = 1.73%, SD = 0.11, n = 8) and absent ($\bar{x}$ = 2.09%, SD = 0.13, n = 6) in December (F = 32.15, P < 0.001).

Seasonal FN was highly correlated with both TDN and DDN (Fig. 14a). Fecal nitrogen was generally about 1% higher than TDN and 2% higher than DDN, with DDN being near zero during most of the winter (Fig. 14b). Fecal nitrogen also was highly correlated with IVDMD (Fig. 14c). Estimates of apparent digestibility, however, calculated by regression from FN (Wehausen 1955), were much higher than the IVDMD estimates (Fig. 15). Relative differences among bi-monthly periods and years were similar for both methods of deriving digestibility though.

Daily Intake

Estimated daily DMI, calculated by the fiber ratio, lignin ratio, and simple IVDMD, was much lower during all bi-monthly periods than when calculated using apparent digestibility calculated by regression from FN (Fig. 16), but exhibited similar seasonal patterns. Estimates of DMI were highest for June, intermediate for August, and much lower for the 4 winter months. Metabolizable energy and digestible protein intake were calculated from DMI, and thus exhibited similar seasonal patterns, but at different scales.

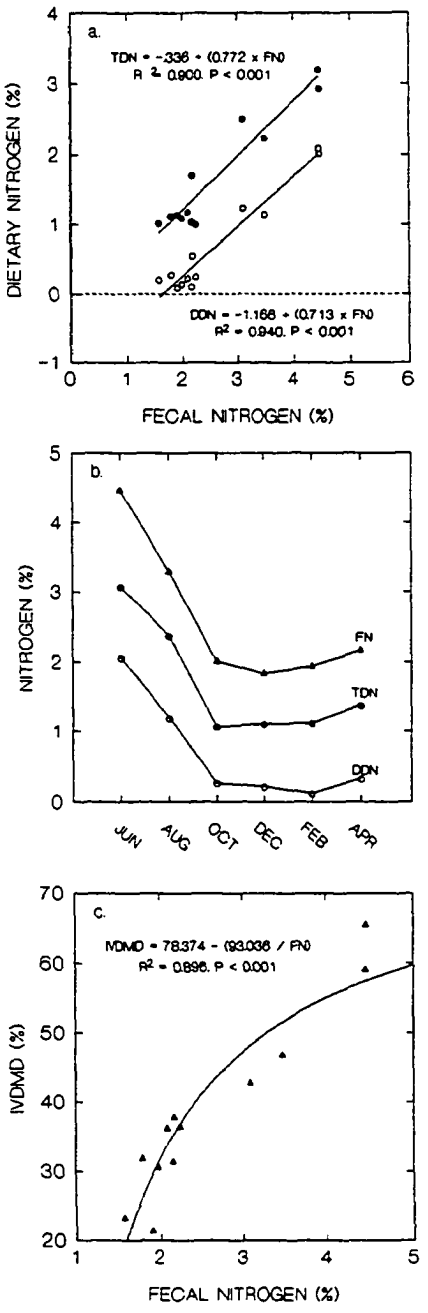

Fig. 14. Relationship between total dietary nitrogen (TDN), digestible dietary nitrogen (DDN) and fecal nitrogen (FN) (a, b) and between in vitro dry matter digestibility (IVDMD) and fecal nitrogen (c) for free-ranging adult female Dall's sheep diets in the northern Brooks Range, Alaska, 1986-1988.

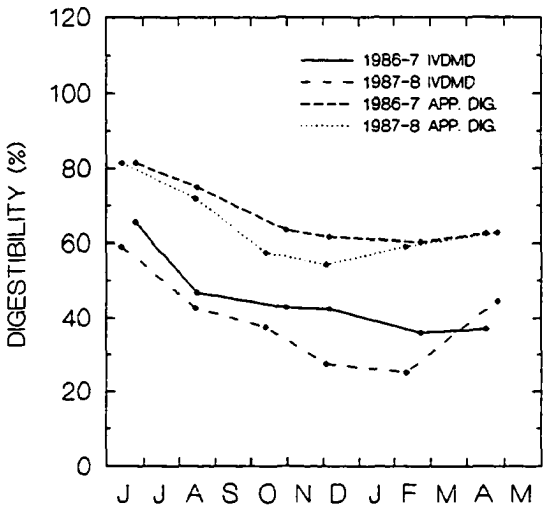

Fig. 15. Bi-monthly apparent digestibility estimated by regression from fecal nitrogen and in vitro dry matter digestibility (IVDMD) in the diet of free-ranging adult female Dall's sheep in the northern Brooks Range, Alaska, 1986-1988.

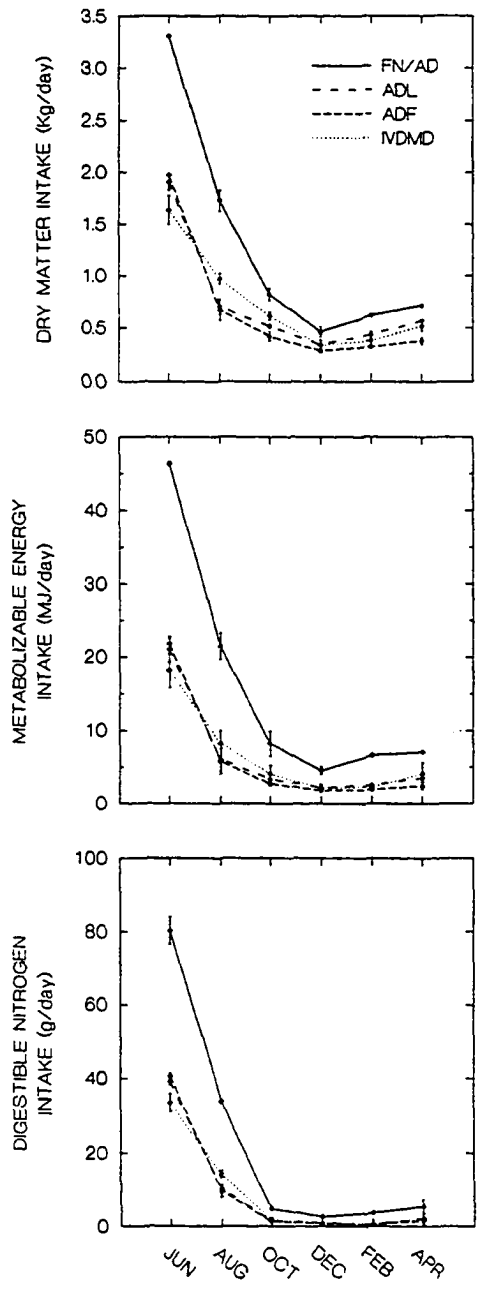

Fig. 16. Bi-monthly dry matter intake, digestible nitrogen intake, and metabolizable energy intake estimated by acid detergent fiber (ADF), acid detergent lignin (ADL), and in vitro dry matter digestibility (IVDMD) ratio methods for free-ranging adult female Dall's sheep diets in the northern Brooks Range, Alaska, 1986-1988.

DISCUSSION

Corrections for Digestibility

In this study, uncorrected diets of Dall's sheep ewes determined by microhistological analyses were significantly different during all seasons from diets for which the effect of differential digestibility was corrected. Consequently, the uncorrected diets microhistological analyses provided a measure of diet composition that was biased toward forages with lower digestibility. In this study, subsequent measures of forage quality also would have been biased. The extent of bias varied seasonally and was related to the difference between least and most digestible foods in the diet. Further, because diets are expressed as percentages, taxa that compose a large proportion of a diet and that have digestibility rates that are either high or low relative to the remainder of the diet will have the greatest effect on bias of the diet as a whole.

Fortunately, forages that are highly indigestible are typically avoided, and so usually affect overall bias less than forages that are highly digestible. Thus, the forb class was responsible for the greatest bias in diets of ewes in the northern Brooks Range when forbs were in highly digestible early phenological stages during spring and summer. Moss was the least digestible forage in winter when most forages were dry, and was most responsible for bias in the winter diets. Most winter forages were relatively similar in digestibility and so bias during this season was generally lower than in summer.

Most studies of diet derived from fecal or rumen samples have not performed digestibility corrections on their data (e.g. Ayres 1986, Seip and Bunnell 1985). Although

accuracy of winter diets may have been reasonable, it is likely that summer diet composition values are inaccurate. We concur with Leslie et al. (1983) that data on uncorrected diet composition be considered an index at best and used for general comparisons only. We believe these data are not suitable for purposes of estimating relative quantity of forage taxa consumed.

Although it is possible that identifiable portions of some extremely digestible plant taxa may be completely destroyed by digestion and thus not observed in fecal samples, we disagree with the recommendation of Holechek and Valdez (1985) that fecal analysis data should be presented without correction for differential digestion. Our results showed that presenting only uncorrected diets can underestimate the importance of the most highly digestible and nutritious forage available to ungulates, namely forbs. We recommend that data on diets from microhistological analyses be presented both in the uncorrected and corrected form, so that direct comparisons with most previous data can be made, while showing land and wildlife managers the importance of the highly digestible forbs in diets of ungulates.

Diet Composition

We observed a distinct seasonal pattern in the diets of Dall's sheep ewes in the north-central Brooks Range. Ewes consumed large quantities of forbs and moderate quantities of grasses, sedges, and shrubs in summer when these plants were in the early phenological stages of growth and their digestibility was high. In autumn, when most

plants became senescent, ewes shifted to increasing quantities of grasses and sedges as a staple winter diet. In the second year of our study, we noted ewes tended to feed on grasses in early winter and gradually shift to other graminoids through mid-winter, then back to grasses in late winter and early spring. The greater use of other graminoids in the early winter of 1986 likely resulted from deep snow and cold that began earlier in 1986 than in 1987. Use of shrub willows in winter was observed most when deep snow made access to other forage difficult. Mosses and lichens were used little, and mosses probably were used accidentally because they were intertwined in the mosaic of the other forage plants.

Similar general seasonal patterns of forage use have been reported in most other year-long studies of Dall's and Stone sheep (Murie 1944, Nichols and Heimer 1972, Luckhurst 1973, Hoefs and Cowan 1979, Seip and Bunnell 1985). Uncorrected diets (Fig. 6) we determined for ewes in the northern Brooks Range were comparable to most of these studies, as well as other summer studies. Each of these studies reported diets in some seasons that were different than those we noted in the north-central Brooks Range. In Denali National Park in the Alaska Range Dall's sheep may eat more willow than did ewes in the northern Brooks Range in summer (Murie 1944, Whitten 1975). Similarly, Dall's sheep in Kluane National Park consumed more willow than did ewes in the northern Brooks Range in spring and autumn, and much more browse in general during winter, especially Artemisia (Hoefs and Cowan 1979). Dall's sheep in 2 of 3 populations in the Kenai Mountains of south-central Alaska (Nichols and Heimer 1972) consumed greater

quantities of willow during winter than did ewes in the northern Brooks Range. These sheep also consumed large quantities of lichens during some winter months, as did Stone sheep in northern British Columbia (Seip and Bunnell 1985) and snow sheep (O. nivicola) in some areas of Siberia (Fedosenko 1986). With the exception of the Stone sheep in northern British Columbia (Seip and Bunnell 1985), forb use reported by each of these studies was similar to forb use in the uncorrected form by ewes in the northern Brooks Range. Seip and Bunnell (1985) reported up to 66% use of forbs in June, which would likely have been much higher had digestibility correction procedures been performed.

A few other studies have included information on summer diets of Dall's sheep. Ayres (1986) reported diets from microhistological analyses of feces in the western Brooks Range that were quite different from elsewhere, with low use of graminoids and high use of browse in summer, especially willow and Dryas. Also, autumn diets of western Brooks Range sheep contained up to 80% lichen, with most of the remainder of the diets being browse. Diets of Dall's sheep in summer in Denali National Park and in the eastern Alaska Range, both derived from visual observation, were dominated by grasses and sedges, but contained substantial quantities of Dryas and willows (Whitten 1975, Winters 1980). Forbs were reported to be a small part of sheep diets in the eastern Alaska Range; however, Winters (1980) used feeding site inspections, which can underestimate use of many forbs that are completely consumed (Whitten 1975), and rumen analyses without accounting for differential digestibility. Dall's sheep in Denali National Park used substantial amounts of forbs in the early growth stages (Whitten 1975).

Diet Selection

Dall's sheep ewes in the north-central Brooks Range exhibited strong selection for forbs in summer, grasses all year, and other graminoids in mid-winter (Fig. 10). This sequence of forage selection is predicted by optimal foraging theory (Pyke et al. 1977, Owen-Smith and Novellie 1982), because forbs are typically the most digestible and highest in protein of forages available during the growing season, and graminoids formed the most available forage that was not well protected by plant chemical defenses such a tannins (Robbins et al. 1987A, 1987B). Further, we observed taller grasses that occur in shrubby areas to retain more green leaves through winter (Whitten 1975, Klein 1990) than did most other graminoids in the study area. This may have led ewes to use both Poa and Festuca selectively over the other graminoids in October, before these species were under deep snow, and to use Festuca in late winter as snow began to melt. Goodson (1991A) reported similar selection by bighorn sheep (O. canadensis) in Colorado for grasses that provided remnant green forage through winter.

Although relative use of the various graminoids changed as winter progressed and grazing reduced forage availability, there was no concurrent change in relative selection among the graminoids. This was likely because both use and availability declined simultaneously, which resulted in the ratio of use to availability that we used to reflect selection remaining unchanged. Similarly, our finding of avoidance of forbs in December and February (Fig. 10) is likely erroneous. We used availability of forage classes from

August in comparisons for the whole year because most forage classes were perennial and basal cover was not expected to change through winter. Fragile forbs, however, likely declined rapidly in availability. Thus, we believe that selection ratings for forbs in winter were probably near zero, but positive rather than negative.

Although Seip and Bunnell (1985) expected forbs to be selected by Stone sheep in northern British Columbia, they concluded that forbs were not selected in spring and were avoided in summer. Forb use, however, was similar in their uncorrected diets to uncorrected diet composition we noted for Dall's sheep ewes in the northern Brooks Range. Therefore, we suggest that, had Seip and Bunnell (1985) accounted for differential digestibility in their diet calculations, they likely would not have concluded that Stone sheep did not follow optimal foraging theory. Hoefs and Cowan (1979) used general selection categories to describe the importance of plant taxa they reported in diets of Dall's sheep at Kluane National Park. Although several plant taxa in Kluane National Park did not occur in the northern Brooks Range, those that did, or were similar to taxa in the northern Brooks Range, attained similar selection rankings by our methods. The findings of Ayres (1986) are perplexing in that the shrub- and lichen-dominated diets are dissimilar to those of all other studies. Although forage availability in her study area, as measured at feeding sites, apparently was similar to that in the northern Brooks Range; sheep in the western Brooks Range inhabited lower elevations with less topographic relief Graminoids and forbs that sheep in our study selected grow on drier sites at higher elevations, and may not have been as widely available in Ayres (1986) study area as they

were at her local feeding sites. Thus, the expected selection for forbs may not have been apparent because she did not measure availability at the study area level,.

Diet Quality

Fecal Nitrogen.-- Fecal nitrogen is correlated with dietary nitrogen for many ruminants, including bighorn sheep (Hebert 1973, Hebert et al. 1984, Irwin et al. 1993) and Stone sheep (Seip 1983). Fecal nitrogen is also correlated with forage digestibility (Leslie and Starkey 1985, Irwin et al. 1993) and may actually be a function of forage digestibility (Wehausen 1995). Consequently, correlations between FN and other forage attributes may be because the other attributes correlate with digestibility (Wehausen 1995).

Although FN may not be a good indicator of either digestibility (Wehausen 1995) or forage nitrogen (Hobbs 1987, Leslie and Starkey 1987, Robbins et al. 1987a) when forage containing phenolic compounds is consumed by ungulates, the technique is useful for comparisons among seasons and populations (Seip 1983, Hebert et al. 1984, Leslie and Starkey 1985, Wehausen and Hansen 1987, Hodgman and Bowyer 1986). Undoubtedly, the strong correlation noted for wild sheep in general results from the largely non-browse diet these animals generally consume (Mould and Robbins 1981).

Our analyses indicated that FN was generally 1% greater than TDN and 2% greater than DDN for ewes in the northern Brooks Range (Fig. 14). Although the correlations between FN and TDN, DDN, and IVDMD were strong (Fig. 14), it is likely

that they were even higher than we estimated. Our measures of dietary N and IVDMD were based on plant samples collected in 1 year and 1 portion of the study area only. Therefore, some of the variability in these forage attributes between years and portions of the study area was lost (Hobbs 1987). We suspect forage collected at the same location and year as feces could have increased the overall correlation.

Although the differences in FN that we reported between foraging conditions with and without snow were significant in both August and December, the second sets of samples were collected only 3 days after the snow conditions changed. Had we been able to wait the 12 days recommended by Hebert (1973) for the rumen microflora to adjust to the new forage, we may have obtained even greater differences, particularly in December when dry forage likely produced longer digestion times (Church 1976:103). Nevertheless, our data support the results of Goodson et al. (1991A) and confirm that snow cover has a significant negative effect on diet quality for wild sheep.

We noted generally higher FN values in the northern Brooks Range than Ayres (1986) reported in 3 areas of the western Brooks Range in summer (Fig. 17a), although by autumn FN values were nearly equal in the 2 studies. The high levels of forbs consumed by ewes in the northern Brooks Range likely produced a higher-quality diet in summer than did the greater amounts of shrubs consumed in the western Brooks Range. Indeed, the Poktovik study area showed the higher FN values than 2 other study areas,

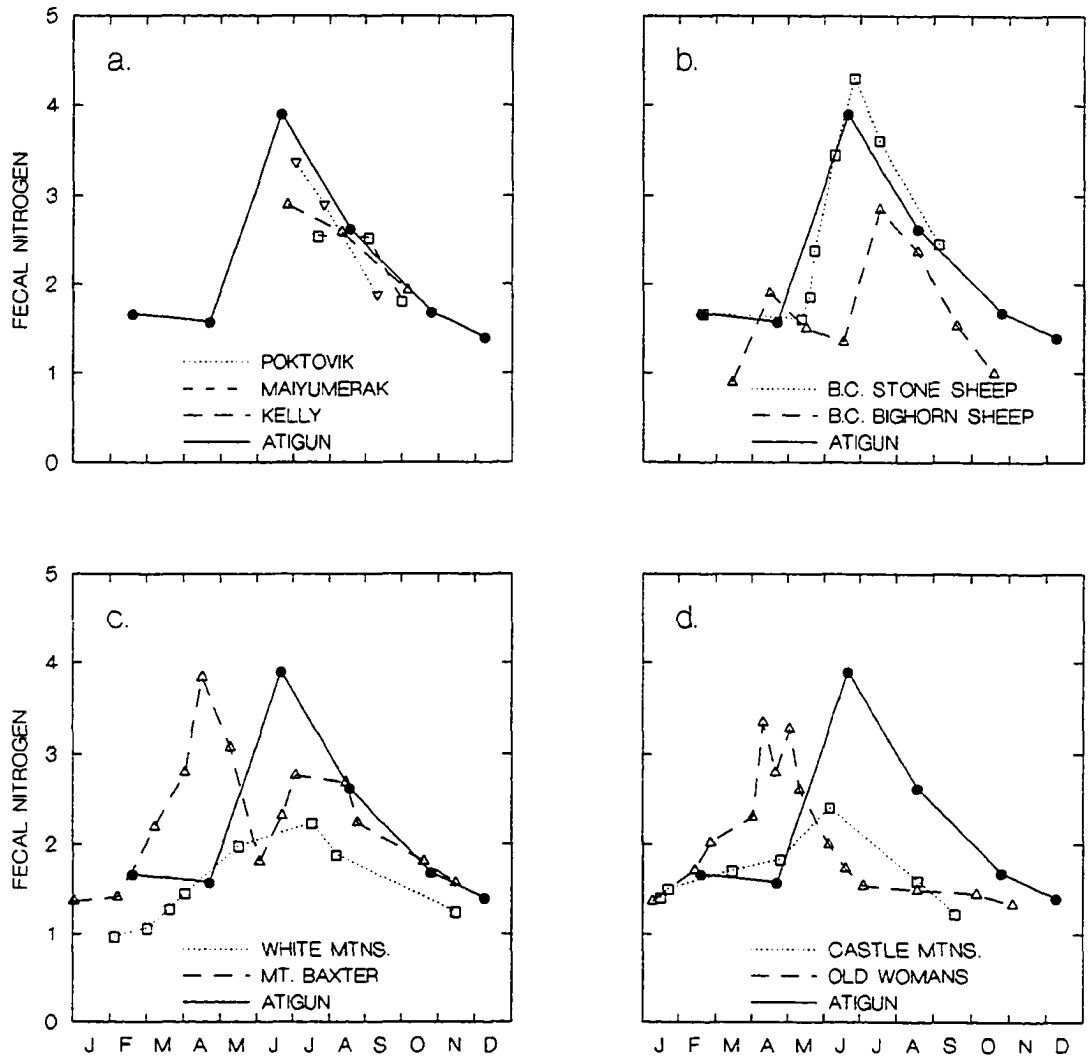

Fig. 17. Seasonal fluctuation of fecal nitrogen levels of free-ranging adult female Dall's sheep in the northern Brooks Range compared with those of Dall's sheep in the western Brooks Range (Ayres 1986) (a), Stone sheep (Seip 1983) and bighorn sheep (Hebert 1973) in British Columbia (b), bighorn sheep in montane habitats in California (Wehausen and Hansen 1987) (c), and bighorn sheep in desert habitats in California (Wehausen and Hansen 1987) (d).

and sheep from that area consumed more forbs than did sheep in the 2 other areas (Ayres 1986).

Values for fecal nitrogen from Stone sheep in northern British Columbia (Seip and Bunnell 1985) were similar to those of Dall's sheep ewes in the northern Brooks Range (Fig. 17b). Peak FN values in northern British Columbia occurred in June and were slightly higher than we reported, possibly reflecting the high levels of forbs consumed by sheep in that study area (Seip and Bunnell 1985). Similarly, FN of Dall's sheep in the central Alaska Range exhibited peak values in June similar to those we reported, but timing of peak FN values was 2 weeks different between 1988 and 1989 as a result of delayed plant phenology from a late snow storm in 1989 (Rachlow and Bowyer 1994). Hebert et al. (1984) simulated the effects of altitudinal migration in bighorn sheep in southern British Columbia and reported that FN peaked in April on the winter range forage and again in July when sheep were fed forage from alpine summer ranges. The diets fed to these bighorns were largely bunchgrasses, and it is possible that naturally foraging sheep could have selected larger quantities of forbs and shrubs, and consequently elevated their FN during most seasons.

Wehausen and Hansen (1987) reported FN values of bighorn sheep on the eastern slope of the Sierra Nevada Mountains in California to be similar to those we noted in the northern Brooks Range with 2 exceptions (Fig. 17c). First, spring green-up was 2 months earlier in the Sierra; and second, sheep there migrated elevationally to alpine areas in early June in part to take advantage of the green-up afforded there later in the summer.

Wehausen and Hansen (1987) also noted FN values for bighorn sheep in the White Mountains in California were much lower during most of the year than in the Sierra Nevada Mountains, and they were also lower than we reported for Dall's sheep ewes. They attributed this to a largely grass diet, resulting from low availability of forbs in the White Mountains.

Fecal nitrogen of desert bighorn sheep in the Old Woman Mountains in southern California (Wehausen and Hansen 1987) were similar to those we reported for Dall's sheep ewes after accounting for latitudinal effects on phenology (Fig. 17d). These sheep were able to take advantage of a large elevational gradient and the prolonged spring green-up that it produced; however, these sheep consumed large amounts of shrubs and shrub flowers during this period rather than forbs as in more northern or alpine areas. As with the White Mountains, bighorn sheep in the Castle Mountains in California had little nongraminoid forage available to them and they were not able to take advantage of the low elevations available to bighorns in the Old Woman Mountains (Wehausen and Hansen 1987).

Forage Nutrients.-- Forage digestibility is highest in young, growing plants, in large part because cell walls have not had a chance to thicken and become lignified (Church 1976), and plant chemical defenses have not been produced (Robbins et al. 1987b). Our estimates of both IVDMD and apparent digestibility reflect this with highest values occurring in June, and rapid declines thereafter (Figs. 8 and 10). The large increase in IVDMD for April 1988 coincided with unseasonably warm weather and an early

breakup that year. We observed that plant material protected by snow cover in drifted areas became available during the early breakup, including some that had been frozen in the green state during the previous autumn (Whitten 1975, Klein 1990). The increase in digestibility was largely responsible for increases in both DE and digestible protein. The lack of a similar increase in FN may be due to a delay between when improved forage became available and when the results became apparent in the feces.

The snow cover in August 1986 had little effect on IVDMD and DE, but had relatively strong effects on both DN and FN (Fig. 13). Available forages in late summer declined more rapidly in protein content than in digestibility or energy content, thus nitrogen was the primary nutrient affected when the ability of ewes to forage selectively was hampered by snow. Conversely, in December 1986 DN levels in the forage already were so low that snow cover could not affect them much, but ewes were inhibited from selecting the most digestible forage and consequently DE was lowered. Similar effects on IVDMD were reported for wintering bighorn sheep in Colorado (Goodson et al. 1991A).

Summer values of IVDMD we reported for Dall's sheep ewes were similar to those of Stone sheep (Seip 1983), and caribou and reindeer (Person et al. 1980), but winter IVDMD levels we observed were lower than in most other studies (Seip 1983, Goodson et al. 1991B), particularly during 1987-88. Ward (1971) reported IVDMD of grasses to be 2-3% higher using inoculum from cattle than from free-ranging elk (Cervus elaphus), but they noted IVDMD of forbs and shrubs was not affected by source of inocula. The rumen inoculum from domestic sheep fed grass hay used in our analyses

should not have affected our IVDMD determinations by more than a few percent. Milchunas et al. (1978) reported that IVDMD was similar to in-vivo digestibility in highly digestible forages, but gave a slight under estimate (1-2%) at low levels of digestibility. They also noted that nearly all digestible dry matter from forbs and shrubs was digested within a 48-hour trial period. Milchunas et al. (1978), however, demonstrated that grass, with its higher percentage of digestible fiber, digested at a slower initial rate and by 48 hours had reached only about 85% of its digestibility after 100 hours, the typical passage time for dry grasses. Even after correcting for short IVDMD times, winter IVDMD was below the 49% required for winter maintenance by Stone sheep (Seip 1983) and 50% required for winter maintenance white-tailed deer (Odocoileus virginianus) (Ammann et al. 1973).

Seasonal and annual patterns we estimated for apparent digestibility were similar to those estimated by IVDMD, yet estimates of apparent digestibility were consistently 20-30% higher than estimates for IVDMD (Fig. 15). Although the regression equation we used to calculate apparent digestibility from FN (Wehausen 1995) was developed using data from domestic sheep, the values we obtained were similar to apparent digestibility measured for captive bighorn sheep on both summer and winter diets (Hebert 1973). The discrepancy between our estimates of digestibility measured by IVDMD and apparent digestibility may have resulted from our inability to be as selective in collecting forage samples as were ewes in foraging, storage of forage samples in the air-dried state prior to IVDMD, use of rumen inocula from domestic sheep that were not well adapted to the

forages Dall's sheep were consuming, inhibitory effects of secondary compounds which could not be counteracted in the digestion tube as well as in the rumen (Person et al. 1980), or a combination of these. Estimates of apparent digestibility based on FN were more indicative of digestibility rates actually experienced by ewes in winter than were IVDMD rates. Presence of secondary compounds in forbs and shrubs that together constitute the bulk of ewe summer diets may have caused IVDMD to underestimate (Person et al. 1980, White and Trudell 1980), and the FN-apparent digestibility method to overestimate (Robbins et al. 1987A) digestibility rates experienced by the ewes.

Daily Intake

None of the methods we used to calculate daily DMI were without flaws. Further, all of the methods were calculated from fecal-excretion values estimated primarily from reproductive ewes in the field (Chapter 2). IVDMD likely underestimated true digestibility, at least in winter, due to the long digestion times of graminoids. The fiber method was likely affected by the same problem in winter because a portion of the ADF present in our forage samples was digested during the IVDMD process, as reported also by Cochran et al. (1986). In our IVDMD trials, lignin actually showed negative digestibility, that is, we measured a greater weight of ADL in the residue from our IVDMD trials than in the original forage. This outcome was likely because a variety of other materials often are inadvertently isolated as crude lignin (Van Soest 1982:120). These can include non-lignin plant products, synthetic products resulting from storage or

processing, and insoluble protein such as hair and skin (Van Soest 1982:120). Although we attempted to correct for apparent negative digestibility of ADL and positive digestibility of ADF when using these forage components as markers to calculate daily DMI from daily fecal excretion rate, the basis of these calculations was still derived from our IVDMD analyses. Consequently, intake rates calculated from ADL, ADF, and IVDMD were quite similar to each other and all much lower than intake rates calculated using apparent digestibility.

In summer, our estimates of DMI calculated using ADL, ADF, and IVDMD were comparable to estimates for Stone sheep (Seip 1983), domestic sheep (Blaxter et al. 1961), and black- tailed deer (Odocoileus hemionus; Hanley and McKendrick 1985) (Table 8). But our estimates of DMI calculated using apparent digestibility were much higher than reported elsewhere, and were likely elevated by secondary compounds in summer diets that were largely composed of forbs and shrubs. And both estimates were higher than measured by Hebert (1973) for bighorn sheep; however, those sheep were fed diets high in grass (65%) in summer that were composed of plant material cut from various natural ranges of sheep. Consequently, we believe digestibility and resulting intake rates measured by Hebert (1973) in summer may have been lower than for free-ranging sheep in the same areas because free-ranging sheep were more likely to select larger amounts of forbs and the more digestible parts of grasses. Intake rates for bighorn sheep in Colorado were in the range of values we estimated for Dall's sheep ewes, but were highly variable within and among years (Goodson et al. 1991B) (Table 8). This high

Table 8. Summary of daily dry matter intake of similar size ungulates including: Dall's sheep ewes, Stone sheep, bighorn sheep, and domestic sheep during various seasons.

Reference	Species	Season	Weight (kg)	Intake (g/day)	
				Whole animal	Per $kg^{0.75}$ body mass
This study	Dall's sheep - IVDMD	December	66	408	17.6
		February	59	512	24.0
		March	56	612	29.9
		June	56	1902	92.9
	Dall's sheep -Ap. Dig.	December	66	464	20.0
		February	59	617	29.0
		March	56	675	33.0
		June	56	3309	161.6
Seip (1983)	Stone sheep	February	61[a]	900	41.2
		May	56[a]	2025	98.9
Hebert (1973)	Bighorn sheep - Migratory	March	37	545	36.5
		July	38	1125	73.9
	Bighorn sheep - Non-migr.	March	28	530	43.3
		July	35	1020	70.9
Goodson et al. (1991B)	Bighorn sheep - 1985	Jan/Feb	57[b]	1025	49.4
		May	57[b]	1400	67.5
	Bighorn sheep - 1986	Jan/Feb	57[b]	1900	91.6
		May	57[b]	2110	101.7
Alldredge et al. (1974)	Mule deer	Winter	59[b]	1164	54.4
		Summer	59[b]	1455	68.0
Hanley and McKendrick (1985)	Black-tailed Deer	Late winter	40[b]	800	50.3
		Late summer	40[b]	1530	96.2
Blaxter et al. (1961)	Domestic sheep	Poor hay	66[a]	1094	47.2
		Good hay	56[a]	1804	88.1

[a] Weight we assumed for calculations.
[b] Hypothetical weight from reference.

variability in intake rates for bighorn sheep may have resulted from the technique of hand clipping "bites" from adjacent plants along the foraging paths of sheep to measure of bite size. Intake rates of mule deer in summer obtained using a Cesium-137 method (Alldredge et al. 1974) were much lower than those we estimated, but were averaged over the whole summer and thus did not represent comparable peak intake values their animals likely consumed during early summer.

Our estimates of DMI by Dall's sheep ewes in winter were lower than measured elsewhere (Table 8). Stone sheep in northern British Columbia provide the most comparable data, yet the estimate for February (Seip 1983) is still higher than we noted for Dall's sheep ewes in February using either method. This may be because Seip (1983) estimated intake from a model which incorporated data from several other studies of bighorn sheep and domestic sheep, and assumed levels of digestibility higher than we noted for ewes in the northern Brooks Range. Winter intake in all other studies also was higher than we reported for Dall's sheep ewes (Blaxter et al. 1961, Hebert 1973, Alldredge et al. 1974, Hanley and McKendrick 1985, Goodson et al. 1991B). Hebert's (1973) animals, however, were confined to metabolism cages in a nonheated building and likely had lower energy requirements than free-ranging animals. Further, digestibility of winter forage also was higher in these studies which took place in more temperate regions where animals were not exposed to the extended winter conditions and darkness that free-ranging ewes in the northern Brooks Range encountered.

Seip and Bunnell (1985) suggested that reduced foraging time in winter was primarily due to the low quality of food that was available at that time of year. We agree, but in the northern Brooks Range, the lowest foraging times and amounts of DMI occurred in December, yet forage quality presumably continued to decline slightly through February and March. We suggest that climatic conditions, particularly hours of available daylight, was a secondary factor affecting time spent foraging, and consequently on DMI. Snow cover largely determined availability of winter forage by limiting access to the best quality forage in winter and by its effect on onset of new spring growth.

Heimer (1980) examined several indices to population quality and concluded that food resource quality is not the sole and perhaps not a major contributing factor to the differences interpreted as indicators of population quality. Data on which he based this conclusion, however, were collected in early and late winter only. Our data show that forage quality is so low as to preclude growth of individuals in winter, and that the only season during which growth is possible is the short summer period. We suspect that had Heimer (1980) examined differences in forage quality between the low and high "quality" populations during summer his conclusions would have been different.

MANAGEMENT IMPLICATIONS

Our results show that when digestibility of some foods in the diet is much higher than that of the remainder of the diet, uncorrected diets determined by microhistological analyses of feces are strongly biased toward less digestible taxa. Thus, use of corrections

for differential digestibility are critical to understanding the diets of Dall's sheep ewes in spring and summer when foods of high digestibility are consumed. When these procedures are followed, forbs will be far more important in the summer diets of Dall's sheep ewes than many previous studies reported. Therefore, the conclusion that Stone sheep do not select forbs in summer, the taxa with the highest protein content and digestibility, in accordance with predictions of optimal foraging theory is likely invalid (Seip 1983, Seip and Bunnell 1985).

Winter forage available to Dall's sheep ewes in the northern Brooks Range was low in both digestibility and protein content. The limited availability of daylight, as well as occasional snow cover on usually wind swept ridges in winter, further limited the ability of these ewes to locate the best available forage. Summer nutrition is important to late winter survival in wild sheep (Hebert 1973) because it allows weight gains to continue into autumn by recycling nitrogen from body reserves (Staaland et al. 1984). This helps to support rumen microflora that available forage in autumn could not support (Hebert 1973). This is especially important in the northern Brooks Range, where our results showed most winter forage has little digestible protein for at least 7 months. Further, the multiplier effect (Seip 1983, White 1983) of small gains in digestibility and DMI on weight gain point out the importance of selective foraging for the most nutritious plants and plant parts during the 4-5 months of spring, summer, and autumn when forages with variable levels of protein are available. Although we agree that the size of most populations of Dall's and Stone sheep is limited by lack of forage availability resulting from snow cover

on winter ranges (Seip 1983, Heimer 1992), our results support the conclusion that forage quality in summer is likely responsible for most differences in rates of body and horn growth of sheep in different populations (Whitten 1975, Winters 1980).

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CHAPTER 4.

SEASONAL ACTIVITY AND ENERGY BUDGETS OF FREE-RANGING ADULT FEMALE DALL'S SHEEP[4]

ABSTRACT

Wild sheep are primarily active diurnally, yet some populations of Dall's sheep (Ovis dalli dalli) occur north of the Arctic Circle where they are exposed to prolonged periods of darkness, including about 50 days near the winter solstice with no direct sunlight and only 3-4 hours of civil twilight per day. We investigated the 24-hour activities of free-ranging adult female Dall's sheep (ewes) in this environment using radio transmitters equipped with activity sensors every other month from June 1986 to April 1988. From these data, activity and energy budgets were estimated. Ewes foraged during all hours of the day during the 24-hour sunlight of summer. Females restricted foraging almost entirely to the light portion of the day near the equinoxes, and foraged during all hours of available light as well as 2.8 (SD = 1.4) hours of the night in December. Total time spent feeding per day varied from 12.9 (SD = 0.6) hours in June to 7.9 (SD = 1.1) hours in December, and, when measured on a daily basis, was negatively correlated ($R_a^2 = 0.58$) with average windchill ($t = 5.97$, $P < 0.001$) and positively correlated with

[4] Prepared for publication as: Hansen, M. C., and D. R. Klein. 1996. Seasonal activity and energy budgets of free-ranging adult female Dall's sheep. J. Wildl. Manage. 00(0):000-000.

daylength, as measured by civil twilight ($t = 2.90$, $P = 0.005$). Ash-free fecal nitrogen (FN) was positively correlated more with activity level on a monthly basis ($R_a^2 = 0.91$, $P < 0.001$, $n = 11$) than with in vitro digestible dry matter (IVDMD) ($R_a^2 = 0.90$), total dietary nitrogen ($R_a^2 = 0.78$), digestible dietary nitrogen ($R_a^2 = 0.87$), or digestible dietary energy ($R_a^2 = 0.80$). Energetics modeling indicated that ewes were in a negative energy balance and lost about 22% of their initial body weight from the end of October until early May. Digestibility of ewe diets increased from 62% to about 75% with onset of the short summer growing period, and this along with the duration of this season were the most critical variable determining weight gain. Digestibility of diets decreased from 61% to 53-55% during periods of deep snow and was the most critical variable determining weight loss in winter. The model also suggested that Dall's sheep ewes were more adapted to use fat to make up for winter energy deficits than are mule deer (Odocoileus hemionus). Live weight of Dall's sheep ewes appears to increase with latitude in Alaska and may be associated with larger fat reserves.

INTRODUCTION

Dall's sheep (Ovis dalli and ancestors) apparently have been resident in the Brooks Range of Alaska for more than 125,000 years (Korobitsyna 1974). Extreme cold, darkness, and limited quantities of low-quality forage during long winters above the Arctic Circle present a formidable challenge for these primarily diurnal herbivores. Further, summer is particularly short at these high latitudes, providing little time for sheep to

accumulate energy reserves for winter. Despite these environmental extremes, the Brooks Range contains large numbers of Dall's sheep, often at high densities (Summerfield 1974, McDonald et al. 1990).

Prior to this study, information on activity patterns of Dall's sheep was limited to the daylight portions of the day and consequently included little information from winter (Whitten 1975, Hoefs and Cowan 1979, Winters 1980, Curby 1981, Rachlow and Bowyer 1994). Yet, winter conditions prevail for the greater part of the year above the Arctic Circle, and at the latitude of our study area the sun did not rise above the horizon for about 50 near the winter solstice.

Knowledge of activity patterns and energy budgets can be used with nutrient intake information in energy balance models to help land and wildlife managers anticipate effects of various management actions. If such models do not include information from the long winter period, however, they are of limited use, as winter is the season of greatest mortality for Dall's sheep (Murie 1944, Whitten 1975, Nichols 1978).

The primary objective of this study was to estimate seasonal activity budgets of Dall's sheep ewes near the northern extreme of their range and produce a model of their annual energy budgets. We then used existing empirical data to calibrate the model, performed a series of sensitivity analyses, and examined the effect of changes in initial body weight and forage digestibility on winter survival. Data on activity also were used to test the following specific null hypotheses: (1) ewes were equally active during all hours of the day; (2) ewes did not change duration of active and resting bouts between day and

night or among bi-monthly (every other month) sample periods; (3) several environmental variables, including daylength, had no effect on proportion of the day ewes spent active; (4) proportion of the day ewes spent active was not affected by annual or individual animal variation; and (5) varying levels of forage quality did not affect the proportion of the day ewes spent active.

STUDY AREA

We conducted field work in the western end of the Arctic National Wildlife Refuge in the northern Brooks Range of Alaska (68.5° N, 149.3° W). The study area was adjacent to the Trans-Alaska Oil Pipeline (TAP) and the Dalton Highway. Day length varied from 24 hours/day for about 60 days near the summer solstice, to no direct sunlight and only 3-4 hours of civil twilight daily for about 50 days near the winter solstice. Daily temperature averaged 10 C in July and -29 C in January. Elevations where we observed ewes ranged from 600 to 1,400 m. Vegetation of the study area included tundra communities dominated by graminoids, Dryas, and dwarf shrubs (Chapter 3).

METHODS

In May, June, and August 1986, we located adult female Dall's sheep visually and recorded activity information by direct observation (Hansen et al. 1992). In October 1986, 4 ewes were captured by tranquilizer gun from a helicopter and fitted with VHF radio transmitters mounted on neck collars and equipped with mercury tip-switch sensors

to record activity (Hansen et al. 1992). In March 1987, 3 additional ewes were captured similarly and fitted with VHF radio transmitters. In October 1987, we recaptured 1 ewe to fit her with a new collar, and captured another to fit with the collar of an animal that had died. These 8 ewes were monitored for a total of 97 entire 24-hour periods at bi-monthly intervals between October 1986 and April 1988 using an omni-directional antenna, receiver, scanner, digital processor, and dual-channel chart recorder geared to run at 40 cm/hour (RA-5, RT-2, TS-1, TDP-2. and TDR-1, respectively; Telonics, Mesa, Ariz.) (Hansen et al. 1992). We examined all data collected when temperatures were lower than -32°C to ensure that mercury tip-switch sensors had not frozen (Maier et al. 1996). Groundtruthing of information was also collected simultaneously by direct observation (Hansen et al. 1992).

At roughly 1-hour intervals, we recorded environmental information at the observers location on the telemetry recorder chart including temperature, wind speed, wind gust speed, wind direction, cloud cover, barometric pressure, and presence of sunlight, civil twilight (sun 6° below level horizon), visible moon, aurora, and precipitation. Windchill was calculated (Glover 1993) as:

$$\text{Windchill} = \left\langle \left[\frac{10.45 + \left(6.686112 \times \sqrt{\text{WS}}\right) - \left(0.447041 \times \text{WS}\right)}{22.034} \right] \times \left(\text{T} - 91.4\right) \right\rangle + 91.4,$$

where WS is wind speed (miles/hour), and T is temperature (°F). Windchill was later converted to Celsius. Time of sunrise, sunset, civil twilight, nautical twilight (sun 12° below the level horizon), moonrise, and moonset were taken from Floppy Almanac

software (U. S. Naval Observatory 1988). Snow cover was visually estimated separately for north and south slopes, ridges, valleys, and cliffs to the nearest 10% for each bi-monthly period.

Diel Activity

We calculated percent of each hour spent active for all activity data collected during the study. Hours with more than 6 minutes of unknown activity were excluded from analyses. Numerous zeros and ones in this data matrix precluded use of parametric statistics, therefore, we used an overall Friedman 2-way analysis of variance (Wilkinson 1990) to test for differences in activity among hours of the day. When the overall test was significant, we used the same test with Bonferroni adjustment of P-values to examine differences between specific hours of interest. We also calculated length of periods of uninterrupted activity and resting (bouts) that occurred during both daylight hours (including civil twilight) and night hours of each bi-monthly sample period. For this analysis short periods of resting (<5 min) within longer periods of activity were considered part of the active bout and vice versa. Standard ANOVA techniques with Bonferroni adjusted pairwise comparisons were used to examine differences among months for active and resting behaviors during both day and night (Wilkinson 1990).

Factors Affecting Activity

Eight periods of 24-hour activity were removed from the data set because they were punctuated by missing data resulting from animals moving out of radio reception or technical problems with the receiving equipment. One 24-hour period of data that indicated low levels of activity was also excluded from analyses because it was the only data from an older ewe that emigrated from the study area and was later found dead. Other 24-hour periods with short (<30-min) gaps in data were included in analyses when activity before and after the gap was the same and it was likely that the activity of the animal had not changed during the period. This resulted in 14 sample periods in May-June, 10 in August, 17 in October, 17 in December, 16 in February, and 14 in April.

To analyze effects of various factors on amount of daily activity, we separated ewe activity into 2 categories: active (feeding, walking, running), and resting (standing [STD], lying with head up [LHU], lying with head down [LHD]) (Hansen et al. 1992). The number of hours of active behavior was summed for each 24-hour sample period and separated into day and night activity based on sunrise and sunset and also on beginning and end of the civil twilight day. Daily values for each environmental variable was calculated averaging hourly readings for each day. We used forward and backward stepwise multiple regression with $\alpha = 0.15$ to enter and remove variables (Neter and Wasserman 1974, Wilkinson 1990). Pearson correlation matrices with Bonferroni adjusted probabilities were examined to determine which variables were intercorrelated, and we eliminated the least significant of these variables from the model (Neter and

Wasserman 1974). We tested for the effect of individual variation among ewes by performing an analysis of variance (ANOVA), and included significant environmental variables as covariates (Neter and Wasserman 1974). Finally, to examine the effect of forage quality on daily time spent active, we averaged all data within each bi-monthly sample period and regressed these against IVDMD, total dietary nitrogen, digestible dietary nitrogen, digestible dietary energy, and FN (Chapter 3). We used a general threshold level of significance of $\underline{\alpha} = 0.05$, and a family level of significance of $\underline{\alpha} = 0.05$ for multiple comparisons.

Energy Model

The conceptual model (Fig. 18) we used was a variation of that developed by Fancy (1986), but used linked computer spreadsheets in our analysis (Appendix I). The time step used was 1 day and all rates have the implied time dimension of day^{-1}. All weights are expressed in kilograms and all energy measures are expressed in megajoules (MJ) unless otherwise noted. Where necessary, calories (cal) were converted to Joules (J) by multiplying by 4.184.

Energy Intake.-- Daily dry matter intake (DMI; Table 9) was calculated from daily fecal excretion (Chapter 2) by 2 methods. The first involved the IVDMD procedure with an extended digestion period of 60 hours. Milchunas et al. (1978) reported that digestibility of grasses after 48 hours was only about 85% of their final digestibility after 100 hours. Dry graminoids composed the bulk of ewe diets during the 4 winter months

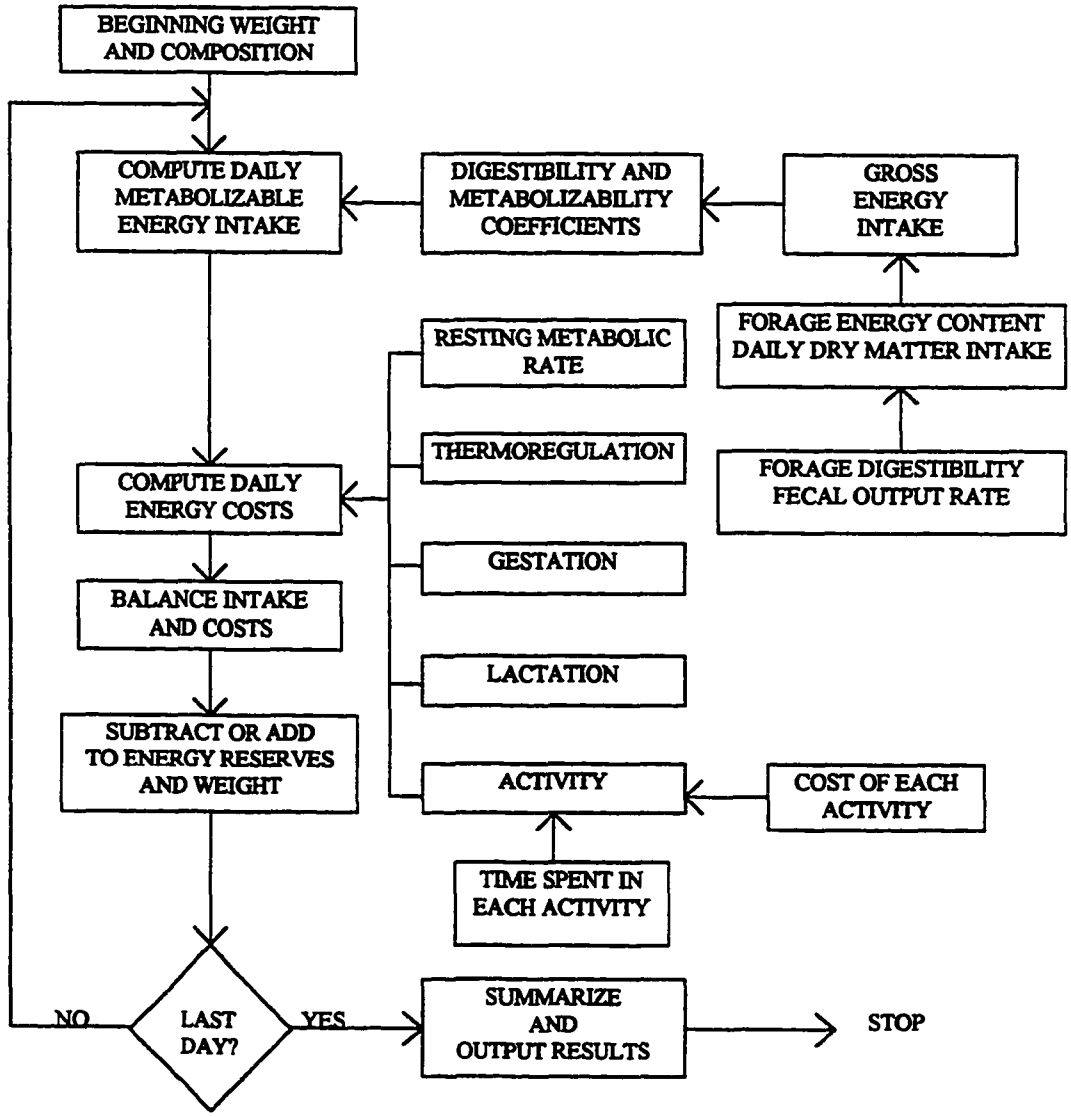

Fig. 18. Conceptual model for simulation of adult female Dall's sheep energy budgets in the Brooks Range, Alaska.

Table 9. Glossary of variables in the order presented in the text.

Variable	Units	Description
DMI	kg/day	Dry matter intake
FEXCR	kg/day	Fecal excretion
DIGEST	%	Forage digestibility
DE	J/g	Digestible energy of the forage
GE	J/g	Gross energy of the forage
ME	J/g	Metabolizable energy of the forage
MEI	MJ/day	Metabolizable energy intake
RMR	MJ/day	Resting metabolic rate
EXMAINT	MJ/day	Energy expenditure for maintenance
H_{ACT}	hr/day	Time spent in each activity
I_{ACT}	-	Energy increment above RMR while standing for each activity
EXGEST	MJ/day	Energy expenditure for gestation
EXLACT	MJ/day	Energy expenditure for lactation
E_t	MJ	Energy content of the gravid fetus
W_o	kg	Total weight of lamb at birth
EMILK	MJ/kg	Energy value of the milk
YMILK	kg/day	Milk yield
BF	%	Butterfat content of the milk
LVWT	kg	Live weight
WTFAT	kg	Weight of fat
WTPROT	kg	Dry weight of protein
WTH2O	kg	Weight of water
WTASH	kg	Weight of ash
WTCPT	kg	Weight of the conceptus
EB	MJ	Energy balance
EFFPROD	%	Efficiency of production for weight gain
EFFMOBIL	%	Efficiency of mobilization fo weight loss
EN2FAT	%	Proportion of energy balance apportioned to/from fat
EN2PROT	%	Proportion of energy balance apportioned to/from protein
EFAT	kJ/g	Energy content of fat
EPROT	kJ/g	Energy content of dry protein

and likely were retained in the rumen longer than 48 hours during these months. Therefore, we divided IVDMD rates during winter by 0.85 to account for the longer rumen residence time in intake calculations (Chapter 3):

$$DMI = \frac{FEXCR}{\left(\frac{1 - IVDMD}{0.85}\right)}.$$

Second, we used fecal excretion (FEXCR) (Chapter 2) and apparent digestibility (DIGEST) estimated from FN (Wehausen 1995, Chapter 3) to calculate DMI as:

$$DMI = \frac{FEXCR}{(1 - DIGEST)}.$$

DMI was calculated bi-monthly for the 2 years of the study using both methods, and daily values were derived for the model by linear interpolation.

Digestible energy of the forage (DE) was determined by subtracting the energy remaining in the residue of the in vitro digestion process from gross energy of the forage (GE) (Chapter 3). Metabolizable energy in the forage (ME) for each bi-monthly period was calculated (Moe et al. 1972) as:

$$ME = (0.96 \times DE) - 1.13,$$

and daily values of ME were derived for the model by linear interpolation. Lastly, daily metabolizable energy intake (MEI) was calculated by multiplying DMI and ME together.

Energy Expenditure.-- Resting metabolic rate (RMR) for standing for each bi-monthly period was calculated for Dall's sheep ewes from a statistical model for bighorn sheep (Ovis canadensis) from the Rocky Mountains (Chappel and Hudson 1980). Dall's

sheep in the Yukon, however, did not seek warmer elevations in winter, even when temperatures reached -37 C (Hoefs and Cowan 1979). Winter pelage of Dall's sheep is extremely insulative with heat transfer rates similar to that of Arctic fox (Alopex lagopus) (Scholander et al. 1950A). Because their thermoneutral zone likely extends to about -40 C (Scholander et al. 1950B), we did not use the higher RMR of bighorn sheep, which have a lower critical temperature between -20 and -30 C (Chappel and Hudson 1980). Daily mean temperature measured during our observation periods were not colder than -30 C during any of our periods, so we used values for bighorn sheep in the -10 to -20 C range.

Hours spent active and resting were split into feeding, walking, standing, lying with head up, and lying with head down, based on error rates between telemetry and observed methods for deriving activity information (Hansen et al. 1992). Proportion of time spent active during which the animal was actually running was calculated from 5 24-hour periods of direct visual observation. Daily energy expenditure for maintenance was then calculated using incremental costs of each activity (Chappel and Hudson 1980, Fancy and White 1985, Dailey and Hobbs 1991) (Table 10) as:

$$EXMAINT = [\,(H_{LHU} / 24) \times (RMR \times I_{LHU})\,] + [\,(H_{LHD} / 24) \times (RMR \times I_{LHD})\,] +$$
$$[\,(H_{STD} / 24) \times (RMR \times I_{STD})\,] + [\,(H_{FEED} / 24) \times (RMR \times I_{FEED})\,] +$$
$$[\,(H_{WALK} / 24) \times (RMR \times I_{WALK})\,] + [\,(H_{RUN} / 24) \times (RMR \times I_{RUN})\,],$$

where H is the number of hours in each activity, and I is the amount that RMR is incremented for each activity.

Table 10. Analysis of model sensitivity to variation in input data for simulation of adult female Dall's sheep energy balance from 23 October 1986 to 23 October 1987 in the northern Brooks Range, Alaska. Values are percent change in daily energy balance and weight before and after a 10% increase in each variable and live weight after 6 and 12 months.

		Daily Percent Change				Live weight (kg)	
	Default	Energy balance		Weight			
Parameter	value	Winter	Summer	Winter	Summer	May 1987	Oct 1987
Default		-	-	-	-	54	69
Digestibility (%)							
June	75.0	1.7	173.0	1.9	254.0	55	102
August	67.0	0.4	52.6	0.2	72.0	54	78
October	63.5	20.9	14.6	17.5	26.3	57	76
December	59.2	29.4	0.2	35.0	0.5	59	74
February	61.3	38.1	1.5	43.4	3.0	61	75
April	62.6	23.0	23.6	26.9	40.6	58	75
Fecal excretion (g/day)							
Summer	612	3.7	46.2	4.8	67.4	54	77
Winter	254	42.1	13.3	43.8	24.3	61	78
Forage GE (kJ/g)							
June	18.9	0	38.8	0	60.9	54	77
December	18.1	22.0	0.2	23.6	0.6	57	72
Residue GE (kJ/g)							
June	16.5	0	-8.1	0	-15.0	54	67
December	17.3	-8.0	-0.1	-8.6	-0.2	53	68
RMR (MJ/day)							
June	13.84	0	-14.9	0	-20.8	54	66
December	8.68	-17.9	-0.2	-19.3	-0.4	52	66
Activity increments							
Feeding	1.17	-21.2	-21.3	-22.1	-35.6	51	62
Walking	1.5	-0.6	-0.6	-0.6	-0.9	54	69
Running	5	-0.2	-0.2	-0.2	-0.3	54	69
Standing	1	-1.4	-1.5	-1.4	-2.5	54	69
Lying head up	0.84	-23.9	-15.9	-25.1	-27.6	51	62
Lying head down	0.75	-0.9	-0.7	-0.9	-1.3	54	69
Activity June (hr)							
Feeding	12.8	0	-2.6	0	-3.5	54	69
Walking	0.3	0	-0.1	0	-0.2	54	69
Running	0.03	0	-0.1	0	-0.1	54	69
Standing	1.1	0	-0.1	0	-0.1	54	69
Activity Dec. (hr)							
Feeding	8.1	-2.1	0	-2.2	0	54	69
Walking	0.2	-0.1	0	-0.1	0	54	69
Running	0.02	-0.1	0	-0.1	0	54	69
Standing	0.6	-0.1	0	-0.1	0	54	69
Lactation							
Milk yield (kg/day)	1.25	0	-7.0	0	-9.0	54	68
Fat content (%)	70	0	-3.5	0	-4.5	54	68
Fattening							
Fat:protein ratio	73:27	0	0	-18.2	-16.5	57	69

Because animals used by Chappel and Hudson were non-reproductive, we calculated energy costs of gestation (EXGEST) and lactation (EXLACT) based on equations for domestic sheep grazing hill pastures (AFRC 1993). A mean lambing date of 1 June was used and date of conception was calculated by subtracting 171 days (Nichols 1978). Total energy content of the gravid fetus (E_t) was calculated (AFRC 1993) as:

$$\log_{10}(E_t) = 3.322 - (4.979 \times e^{-0.00643\,t}),$$

where t is time in days since conception. Daily energy retention then was calculated as:

$$EGEST = (0.25 \times W_o) \times [E_t \times (0.07372 \times e^{-0.00643\,t})],$$

where W_o is the total weight of lambs at birth in kg. Similarly, EXLACT was calculated as the product of energy value of the milk (EMILK) and milk yield per day (YMILK). EMILK was calculated from the formula (AFRC 1993):

$$EMILK = 0.0328[BF] + 0.0025d + 2.2033,$$

where BF is butterfat content in g/kg, and d is the number of days since beginning of lactation. BF was set to 7% (AFRC 1993, Chen et al. 1965). YMILK was estimated by interpolation between values given by AFRC (1993) for a domestic sheep with 1 lamb grazing hill pastures (Appendix I) and checked against values given by Oftedal (1985). Finally, EXGEST and EXLACT were added to EXMAINT to derive total energy expenditure (EXTOTAL).

Weight Dynamics.-- The model calculated total live weight (LVWT) from its component parts: fat weight (WTFAT), dry weight of protein (WTPROT), water weight (WTH2O), ash weight (WTASH), and conceptus weight (WTCPT) separately. Changes

in alimentary fill were not accounted for, other than by WTH2O. When the animal was in a positive daily energy balance (EB), energy was converted to weight gain with an efficiency of production (EFFPROD) calculated from GE and ME (AFRC 1993) as

$$EFFPROD = (0.78 \times (ME / GE)) + 0.006.$$

Conversely, when EB was negative, energy was converted to weight loss with an efficiency of mobilization (EFFMOBIL) of 84% (AFRC 1993). Initially energy was partitioned to fat (EN2FAT) (27%; Torbit et al. 1985) at the rate of 39.75 kJ/g (EFAT) (van Es 1977) and to protein (EN2PROT) (73%; Torbit et al. 1985) at the rate of 23.85 kJ/g (EPROT) (van Es 1977). Later, during the calibration phase, the proportions of energy partitioned to fat and protein were adjusted to 81.5% fat and 18.5% protein. If WTFAT dropped below 1% of LVWT, we assumed that all energy catabolized to make up further energy deficits came from protein (Torbit et al. 1985). Associated changes of water in lean tissue were calculated using the ratio of 29% protein to 71% water (van Es 1977). Weight of ash was held at a constant 4.4% of LVWT (Torbit et al. 1985). WTCPT was calculated from EGEST similarly, but the proportion of energy made up of fat (23.2%) and of protein (76.8%), as well as the ratio of protein (17.8%) to water (82.2%) in lean tissue, were derived by trial and error until the proportions of protein (16.4%) and fat (3.0%) in kg of the gravid fetus matched those in the newborn domestic lamb (Oftedal 1985).

Calibration and sensitivity analyses.-- We calibrated the model using 4 types of empirical data. First, live weights of animals captured for radio telemetry purposes were

available for 24 October 1986, 27 March 1987, and 23 October 1987. We set live weight equal to the known mean weight on 24 October 1986 ($\bar{x}$ = 68.7, SD = 4.5 kg, n = 3) and then tested whether the model successfully predicted the measured weight the following March ($\bar{x}$ = 56.0, SD = 1.7 kg, n = 3) and October ($\bar{x}$ = 69.0, SD = 4.2 kg, n = 2). Second, field data for model input covered 2 annual cycles and we were able to test whether the model predicted weight changes over this extended time similar to those expected from recorded environmental conditions for those 2 years. Third, each of the 3 marked animals that was tracked for multiple years bore lambs in 2 of 3 years. Therefore, we determined that the model allowed similar frequency of lambing. And fourth, we set the energy mobilization ratio equal to that for mule deer (73% fat : 27% protein) (Torbit et al. 1985) and tested whether the model predicted body composition changes reported for Dall's sheep ewes in 2 areas of the Alaska Range in November (14% fat : 12.65% protein) and in late April (5% fat : 11.75% protein) (Heimer 1980).

These tests suggested that estimates of some model input variables were inaccurate. Therefore, input values for forage digestibility and fat:protein mobilization ratio were adjusted by trial and error until the model successfully predicted weight change from October 1986 to March 1987 to October 1987, fat and protein changes from November to late April, and changes over the 2 year cycle were consistent with producing 2 young in 3 years. In no instance were variables adjusted beyond their estimated 95% confidence limits. The final model continued to have the setpoint on 24 October 1986, and the operation of the model was extended backward to April 1986 and forward to June

1988 by reusing data from April 1987 and June 1986 to produce output covering 2 entire years. Finally, we conducted a series of sensitivity analyses on input variables by increasing each variable 10% while all others were held at the calibrated default values.

Simulation of severe conditions.-- December 1987 produced snow conditions that limited forage availability, and consequent digestibility, on the study area. We used the model to examine the additional effect of limited forage availability in other bi-monthly periods of that year by using the default model inputs and then systematically changing digestibility in summer or winter. For these simulations, we assumed that the model animal was not likely to survive weight loss in excess of 35% (de Calesta et al. 1975) or loss of protein in excess of 1/3 of total stores (Cahill 1970).

Live weight of Dall's sheep inhabiting the Brooks Range appeared greater in both autumn and spring than for Dall's sheep populations in the Alaska Range (Heimer 1980) and in southern Alaska (Nichols 1978). Consequently, we examined the effect of changes in overall body size for ewes while keeping fat constant, as a proportion of body composition. In another set of simulations we explored the effect of increased weight as a result of increased fat, as a proportion of body composition.

RESULTS

Diel Activity

Ewes were generally active during the daylight hours in all bi-monthly sample periods (Fig. 19), and there were significant differences in activity among hours during all bi-monthly periods (Friedman > 59.3, P < 0.001). Civil twilight was generally a transition period, and ewes usually rested during the dark hours of the day. Nonetheless, they exhibited several slight exceptions to this pattern. In April, ewes were not active during all daylight hours. Activity remained moderate during the first 3 hours following sunrise rather than shifting to high levels of activity immediately and ewes reduced activity about 2 hours prior to sunset (Fig. 19). Although ewes in June generally reduced their activity between 0100 and 0700 hours, they showed no distinct shift between active and resting behaviors. Although virtually no activity occurred during the dark hours in either April or August, ewes were active to some extent during many of the dark hours in October, December, and February (Fig. 19). Ewes in October spent about 20% of the hours between 2300 and 0400 hours active. And in December, ewes not only increased their activity during nautical twilight, prior to the beginning of civil twilight; but they exhibited 2 minor peaks of activity around midnight and 0500 hours. Two similar but less prominent peaks occurred in February. Although the Friedman test failed to show a difference because ewes were active through many of the hourly samples (Friedman < 2.72 for all hours, P > 0.099), ewes tended to be slightly less active at solar

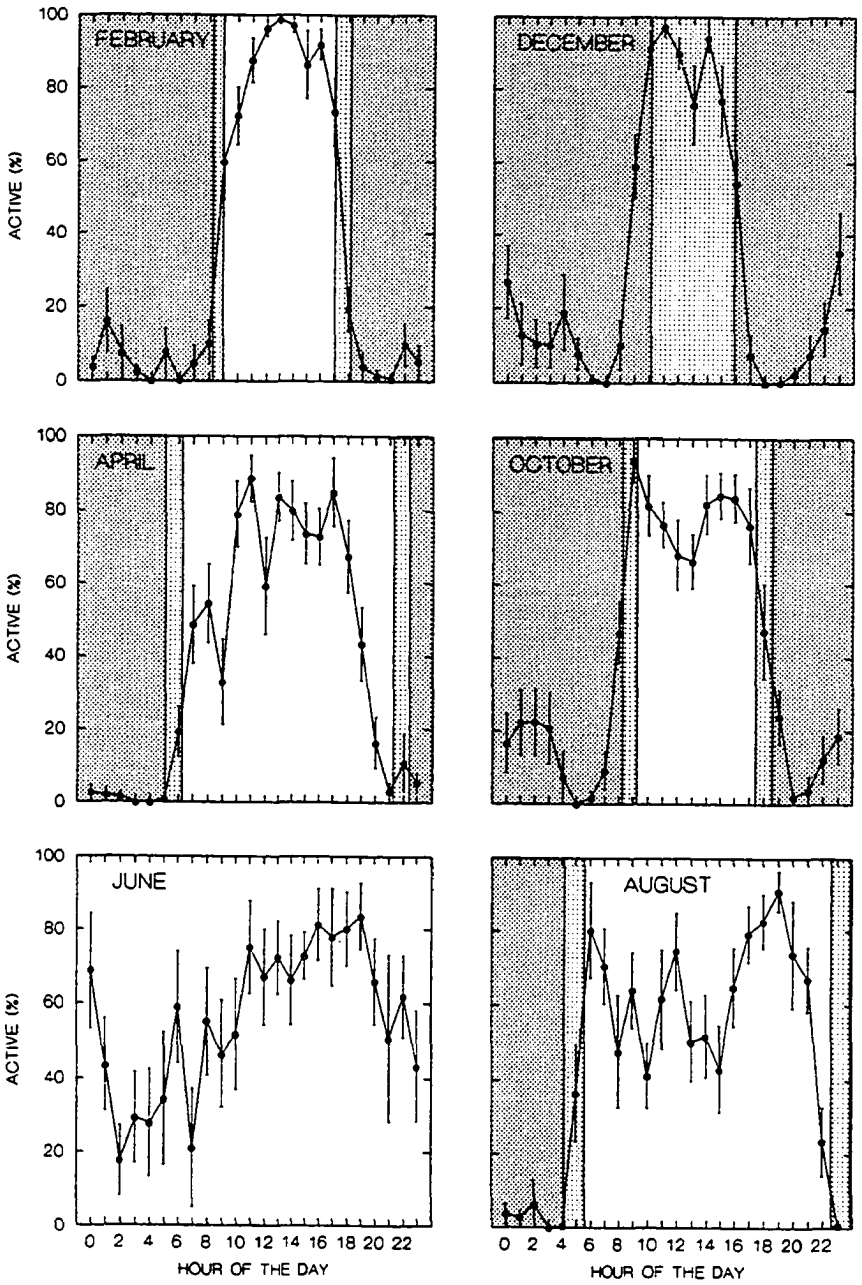

Fig. 19. Mean percent of each hour (0 = midnight) spent active by free-ranging adult female Dall's sheep during February, April, June, August, October, and December during 1986-1988 in the Brooks Range, Alaska. Dark shaded areas represent darkness and light shaded areas represent civil twilight, and vertical bars are standard errors.

noon (1250 AST) during October and December than either earlier or later in the daylight period (Fig. 19).

Bout length for active behavior during the day was different among months ($F = 12.5$, $n = 363$, $R^2 = 0.149$, $P < 0.001$), and was higher in February than in any other month ($P < 0.027$) (Fig. 20). Length of active bouts in daylight reached a minimum in June, then increased again by October when length of active bouts was higher than in April or June ($P < 0.018$). Length of daylight resting bouts showed the reverse trend ($F = 4.37$, $n = 329$, $R^2 = 0.063$, $P = 0.001$), with June being higher than either February ($P = 0.016$) or October ($P = 0.014$) (Fig. 20). At night, length of resting bouts was highest in winter and lowest in August, but because of high variation within bi-monthly sample periods differences were not significant ($F = 1.54$, $n = 95$, $R^2 = 0.08$, $P = 0.184$) (Fig. 20). Length of active bouts at night was different ($F = 4.48$, $n = 97$, $R^2 = 0.163$, $P = 0.002$); however, with April bout lengths being shorter than in October ($P = 0.024$) or December ($P = 0.004$) (Fig. 20).

Factors Affecting Activity

Of the 11 environmental factors examined, only average windchill ($t = 5.97$, $P < 0.001$) and daylength measured between sunrise and sunset ($t = 2.90$, $P = 0.005$) were in the final regression model ($R_a^2 = 0.58$) to predict total time spent active per day. Windchill and daylength were intercorrelated ($R^2 = 0.65$, $P < 0.001$) because lower temperatures typically occurred on short winter days. Daylength measured by civil

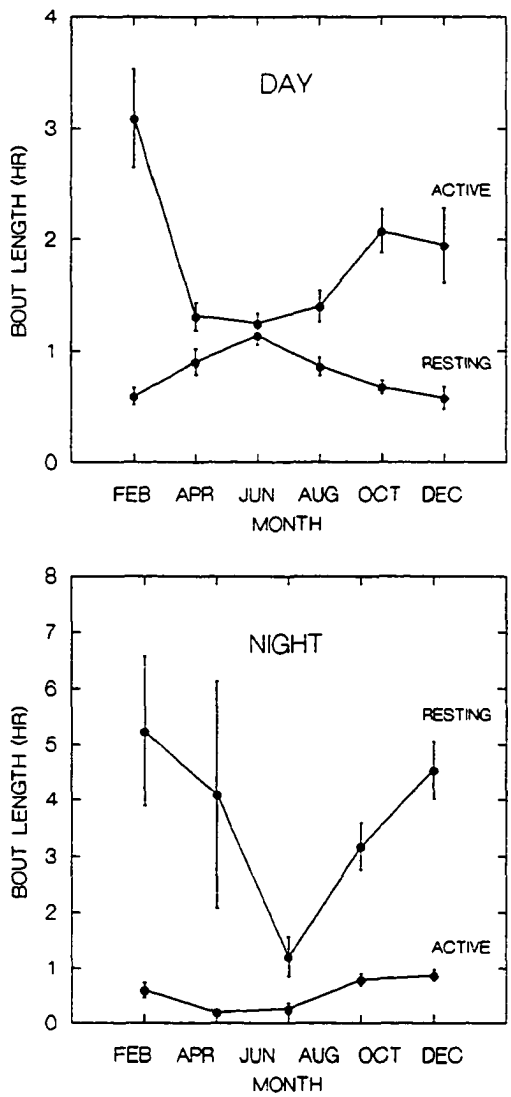

Fig. 20. Mean seasonal bout length of active and resting behaviors with standard errors of free-ranging adult female Dall's sheep during day and night in the Brooks Range, Alaska, 1986-1988.

twilight was not as closely related to time spent active per day ($t = -1.92$, $P = 0.058$) as was daylength measured from sunrise to sunset.

The ANOVA including individual ewe as a blocking variable and both daylength and windchill as covariates indicated that individual variation was significant ($F = 3.85$, $n = 82$, $P = 0.001$) and R^2 of the overall model increased to 0.73. When only those ewes for which data from more than 6, 24-hour periods were included, however, no difference occurred among individuals ($F = 0.368$, $n = 71$, $P = 0.831$).

We had too few observations in some ANOVA cells to include blocking variables for both individual ewe and whether the ewe had a lamb at heel, but the effect of having a lamb at heel when daylength and windchill were included as covariates was significant ($F = 7.10$, $n = 78$, $P = 0.009$) and explained nearly as much additional variation as did the individual ewe ($R^2 = 0.69$). Having a lamb at heel, however, affected activity levels in February ($t = 3.46$, $n = 16$, $P = 0.004$) and August ($t = 6.81$, $n = 10$, $P < 0.001$) only (Fig. 21), and no effect occurred for April ($t = 0.62$, $n = 14$, $P = 0.55$), October ($t = 0.52$, $n = 16$, $P = 0.61$), or December ($t = 0.06$, $n = 15$, $P = 0.95$). The sample of ewes without lambs in June was too small to test this effect. No difference in activity level occurred between the 2 years of the project ($F = 0.84$, $n = 78$, $P = 0.363$).

All of the forage quality measures we tested were inter-correlated (Pearson $R^2 > 0.84$, $P > 0.014$); consequently, we included only FN in our regression model ($t = 10.16$, $n = 11$, $R_s^2 = 0.91$, $P < 0.001$) (Fig. 22) because it was more highly correlated with activity level on a monthly basis than was IVDMD ($R_s^2 = 0.90$), total dietary

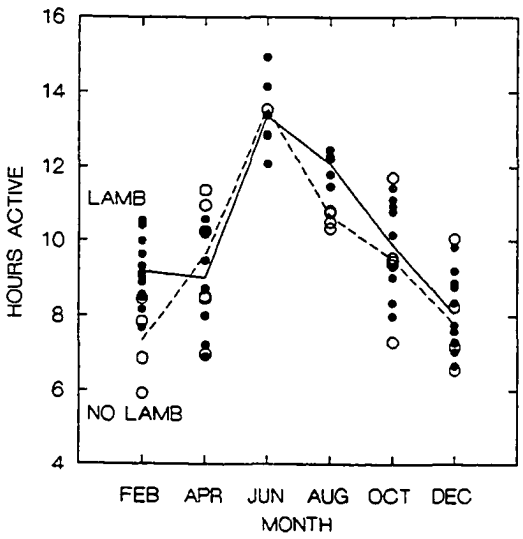

Fig. 21. Mean hours of active behavior seasonally for free-ranging adult female Dall's sheep with and without lambs in the Brooks Range, Alaska, 1986-1988.

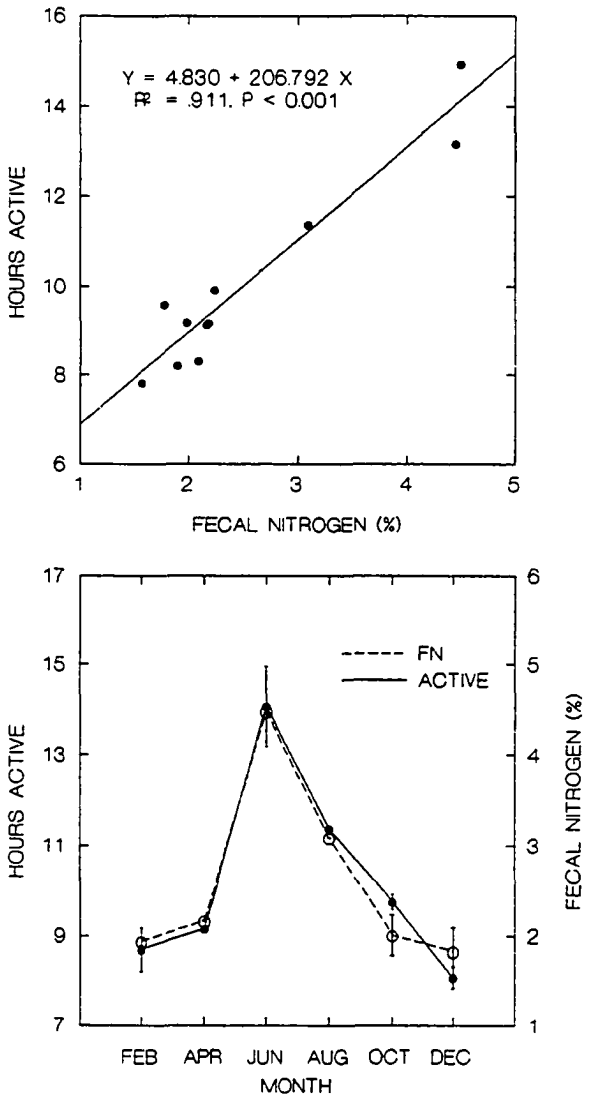

Fig. 22. Relationship between percent ash-free fecal nitrogen (FN) and hours spent active with standard errors by season for free-ranging adult female Dall's sheep in the Brooks Range, Alaska, 1986-1988.

nitrogen ($R_a^2 = 0.78$), digestible dietary nitrogen ($R_a^2 = 0.87$), or digestible dietary energy ($R_a^2 = 0.80$). Finally, we combined windchill and daylength in the model with FN, but only average windchill increased ($P = 0.10$) the explained variability ($R_a^2 = 0.93$).

Energy Model

Calibration and sensitivity analyses.-- Our initial run of the model used rates of digestibility estimated by IVDMD, but the model predicted extreme weight loss even in summer. We suspected that the IVDMD underestimated apparent digestibility, and so we calculated the model using apparent digestibility rates estimated from FN (Wehausen 1995). These digestibility estimates yielded weight gains and losses that were roughly equal within an annual cycle. Seasonal oscillations, however, did not quite match known weight changes from October 1986 to March 1987 and October 1987. To increase winter weight loss between October 1986 and March 1987 to that measured in the field, we lowered the digestibility rate for December to the average between estimates with and without snow for that month (59.2%). This left summer growth rates too high to return the model animal to our measured October 1987 weights, so we lowered digestibility rates for June (75%) and August (67%) to intermediate between estimates from IVDMD and by FN regression.

After these changes in values of input variables, the model produced weight changes consistent with those expected from recorded weather and snow conditions over the entire 2 year period (Fig. 23). The model also suggested that lambs could be born in

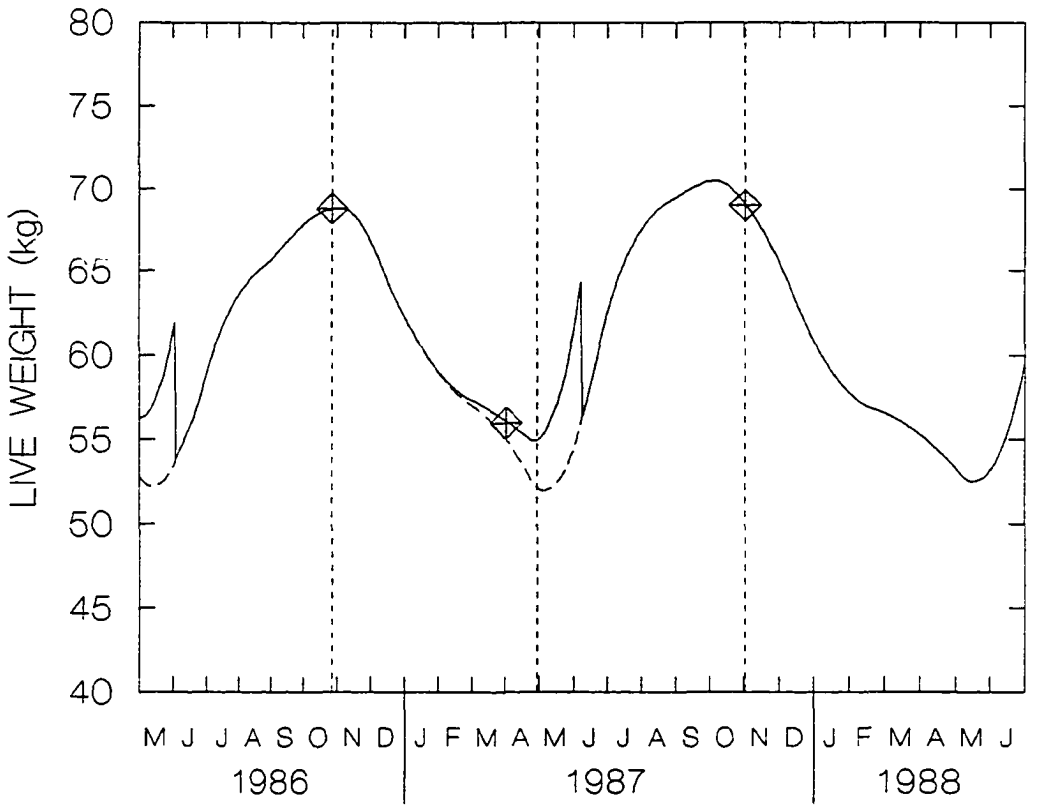

Fig. 23. Simulated live weight (solid line) and maternal weight (dashed line) of an adult female Dall's sheep from May 1986 to June 1988. Diamond symbols represent field measurements of live weight used for model calibration, and vertical dashed lines represent the set point, and 6-month and 12-month checkpoints used in sensitivity analyses.

the first 2 years, but not in the third year as live weight dropped to 46 kg by early May 1988 (Fig. 23) and percent body fat dropped to about 3%. The primary difference between the 2 years of model simulation was that digestibility in October and December 1987 was about 5% lower than in the previous winter, which lowered energy intake and caused the model ewe to begin losing weight earlier in the winter (Fig. 24).

When the ratio of fat to protein in early November was set equal to that reported for Dall's sheep ewes in the Alaska Range (14% fat : 12.6% protein) (Heimer 1980), the ratio of remaining fat to protein reported for Dall's sheep ewes in the Alaska Range in early May (9.0% fat : 12.2% protein) (Heimer 1980) was reached by our model ewe in mid-February. To attain this fat:protein ratio with a weight loss similar to that of ewes in the Alaska Range, we had to adjust the ratio of energy metabolized from fat to 81.5% and from protein to 18.5%. By early May 1987, the model ewe had reached a ratio of 4.5% fat : 11.7% protein, but still weighed 5 kg more than Alaska Range ewes (55 kg). Nonetheless, weight of Alaska Range ewes in early November was 59 kg (Heimer 1980), much lighter than our measured weights of northern Brooks Range ewes at that season (69 kg).

Sensitivity analyses showed that the model input variables that produced the greatest effect on live weight change were digestibility, fecal excretion, and GE of the forage (Table 10). Of these changes in June digestibility had an effect over 3 times greater than any other input variable. GE of the IVDMD residue, RMR, activity increments of feeding and lying with head up, the most frequently occurring activities, as

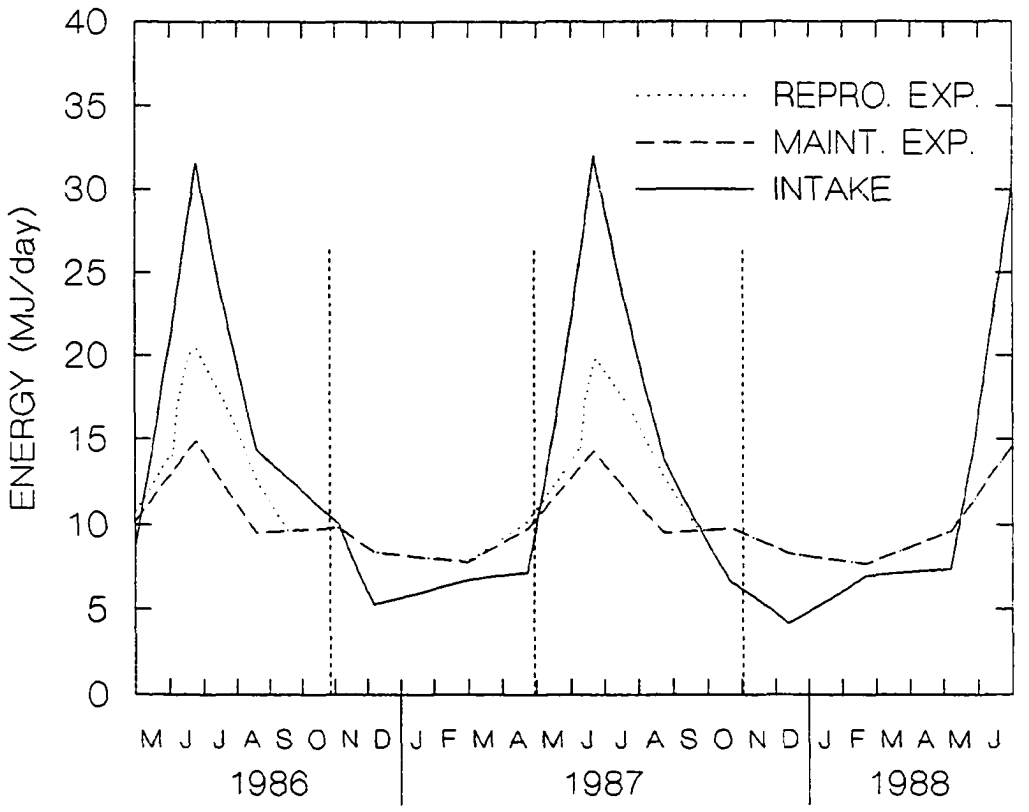

Fig. 24. Simulated energy intake, energy expenditure for maintenance, and energy expenditure for reproduction of an adult female Dall's sheep between May 1986 and June 1988 in the Brooks Range, Alaska. Vertical dashed lines represent the set point, and 6-month and 12-month checkpoints used in sensitivity analyses.

well as ratio of fat to protein deposited or metabolized all had moderate effects on energy balance and weight change. Changes in milk yield and fat content of the milk had little effect on weight change, although changes in number of hours spent in each activity had almost no effect.

Simulation of severe conditions.-- We used values of input variables from the second year of our field data as default values in these simulations. During that winter, digestibility of ewe diets in December was reduced to 53% by snow that limited forage availability. The first series of simulations examined the effect of reduced summer digestibility on likelihood of winter survival. Reduced digestibility in June from 75% to 70% reduced peak autumn weight of the model animal from 70.5 kg to 63.1 kg and body fat from 14.7% to 11.5%. The reductions in both live weight and fat were carried through the winter, and not until June was the animal able to begin building up weight and fat reserves. Minimum fat level reached was 3.1% in mid-May (Fig. 25). When digestibility of the August diet also was reduced (from 67% to 60%), peak autumn weight dropped to 57.9 kg with only 8.7% fat. Body fat nearly reached the 1% level by May after which further energy deficits would have been made up solely by protein catabolism (Fig. 25).

The second series of simulations examined the effect of winter conditions more extreme than the default year with reduced digestibility in December alone. Reduction of October digestibility from 63% to 53% and February digestibility from 61% to 53% forced the animal into weight loss by mid-October rather than later in November as with

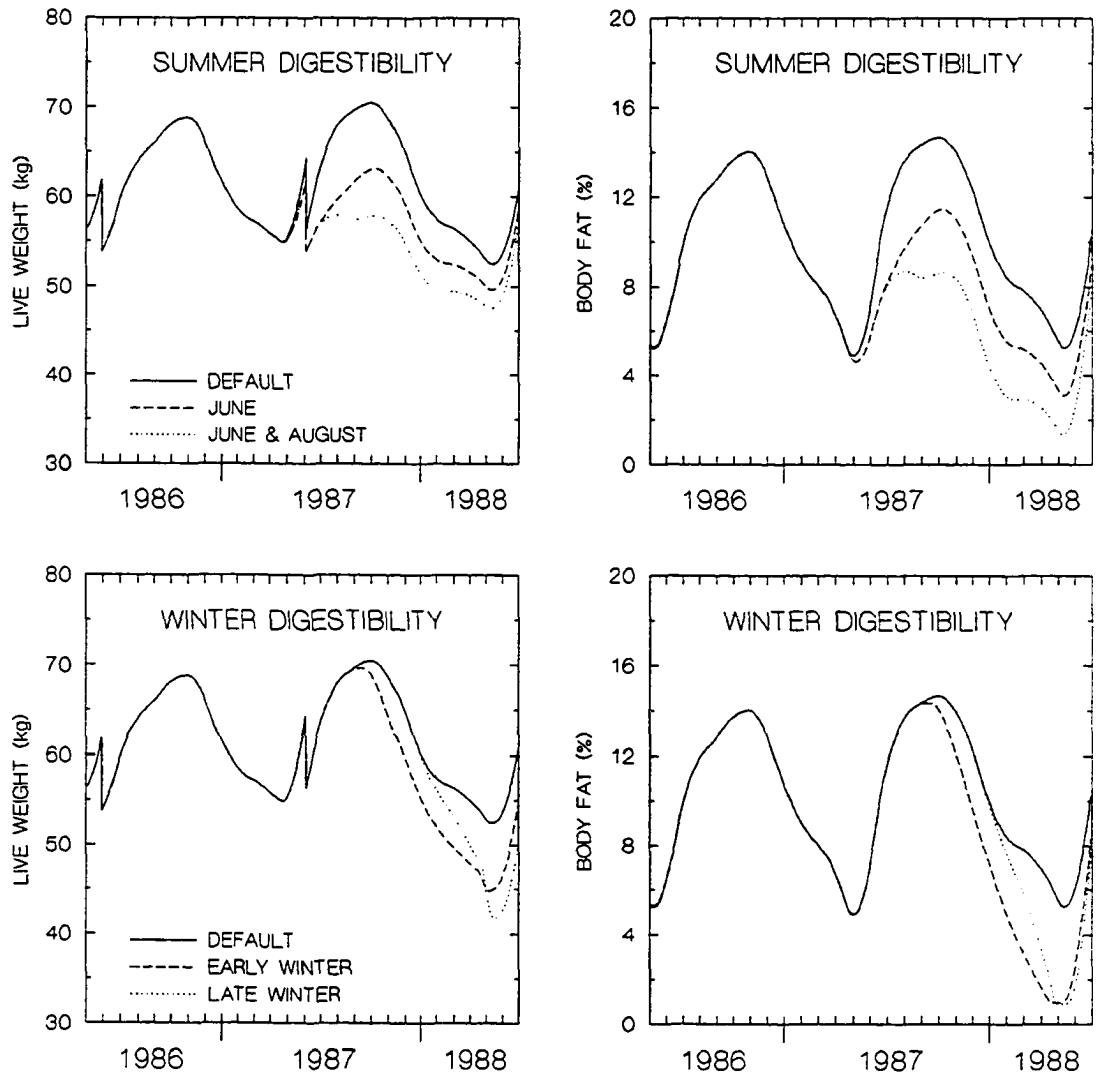

Fig. 25. Simulated live weight and percent body fat of an adult female Dall's sheep between May 1986 and June 1988 in the Brooks Range, Alaska under default conditions and with reduced summer and winter forage digestibility.

the default model animal (Fig. 25). The accelerated weight and fat loss continued until mid-May when the model animal would likely have succumbed to 24 days of forced protein catabolism and weight loss of 35%. Similarly, when February digestibility was reduced from 61% to 53% and April digestibility was reduced from 63% to 53% the model animal would not likely have survived protein catabolism for 27 days and weight loss of nearly 40% (Fig. 25).

The third set of simulations examined the effect of initial body weight on the ability of the model animal to survive winter. Weight of the newborn lamb was kept constant at 4 kg for these model runs. There was little effect of lower initial body weight on fat reserves as a proportion of body composition following the winter. Animals beginning the winter at 69, 60, and 50 kg and 14 % body fat all ended the winter with minimum fat levels in May of 5-6 % (Fig. 25). Model animals with lower initial body weight did not gain as much weight in summer, however, as did the default model animal relative to the loss of fetal tissue.

The last set of simulations, which used varying levels of body fat while live weight was held constant, suggested that reduced peak body fat reserves in autumn (10%) were not sufficient and the model ewe had to rely solely on protein reserves for energy for about 10 days the first spring (Fig. 26). Although the model animal was nearly as heavy as in the default simulation by the following autumn, it had only 12% body fat. Consequently, during the second winter, with reduced digestibility, the model ewe lost more weight and fat than the default animal and would not likely have been able to

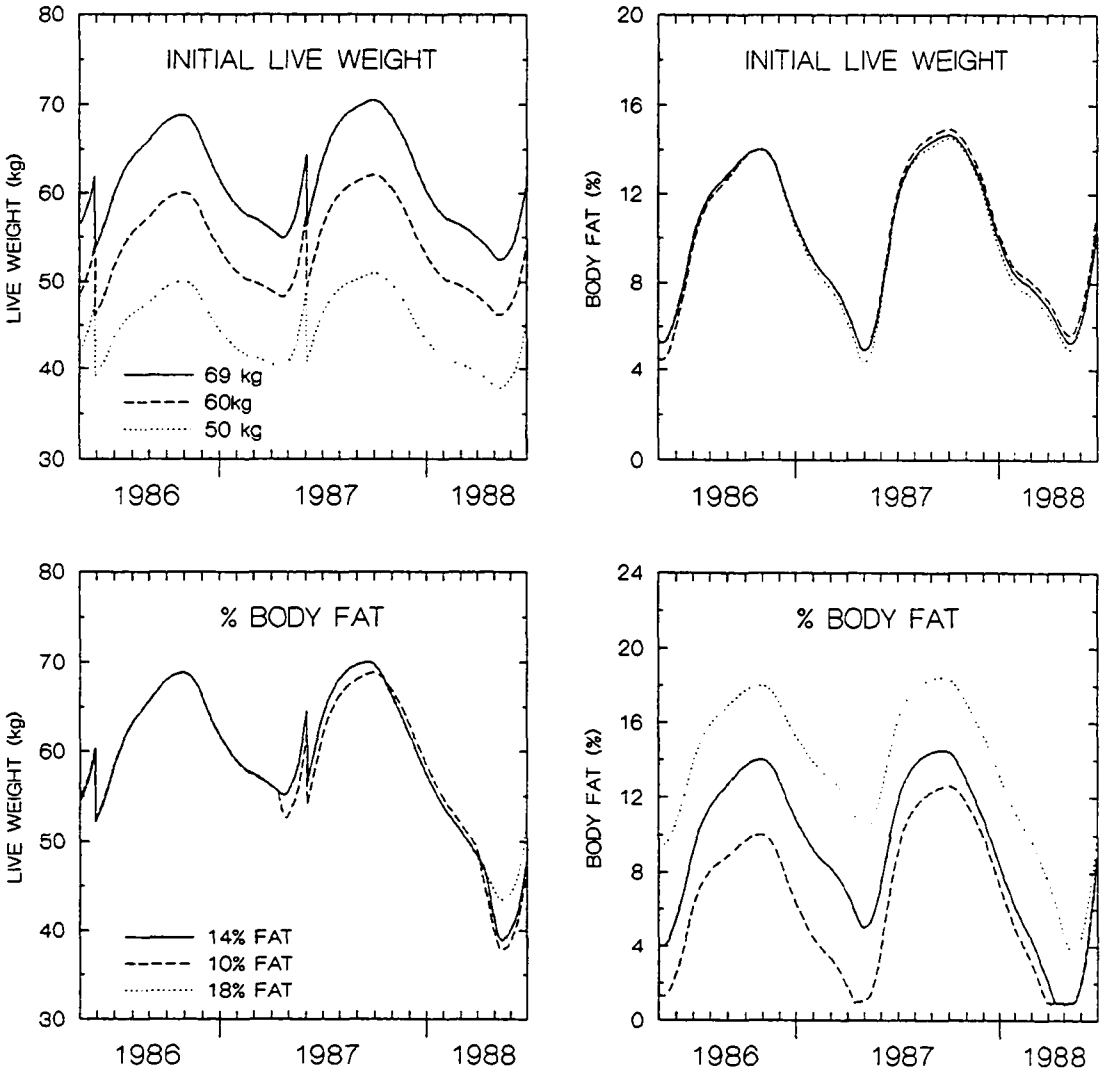

Fig. 26. Simulated live weight and percent body fat of an adult female Dall's sheep between May 1986 and June 1988 in the Brooks Range, Alaska under reduced winter forage digestibility conditions and with differing initial weights and constant weight with differing percent body fat contents.

survive on protein reserves for what was estimated to be 48 days. For the other simulation in this set, we increased fat reserves in the first autumn (18%) and noted that the model ewe likely would have survived the harsh winter of reduced digestibility with minimum body fat reserves of 4%, but a 35% weight loss.

DISCUSSION

Diel Activity Pattern

The pattern of diurnal activity we reported for Ewes near the northern extreme of their range is similar to that of other Dall's sheep (Whitten 1975, Nichols 1978, Hoefs and Cowan 1979, Winters 1980, Curby 1981). Although our data confirmed the presumed tendency of Dall's sheep to rest primarily during dark hours (Whitten 1975, Nichols 1978, Hoefs and Cowan 1979, Curby 1981), we noted that during the winter ewes were active during night for up to 4.4 hours. Most of this activity appeared to be spent feeding, although ewes also likely increased their internal heat production through this activity as well. Nocturnal activity was highest in December when light conditions were lowest and ewes presumably were forced to forage at night to increase energy intake even though foraging efficiency was likely reduced under these conditions. Ewes took advantage of the low light levels during nautical twilight for much of this activity, but foraging did occur throughout the night. Night activity constituted about 35% of daily activity in December, the remainder occurring mostly during civil twilight. Thus, foraging at night

was a key factor that allowed ewes to minimize weight loss during the extended darkness of December.

In early summer, both the diel activity and length of foraging and resting bouts for caribou in central Alaska (Maier and White, in prep.) were similar in length to those for Dall's sheep in the Brooks Range. In contrast to sheep, however, caribou in central Alaska displayed winter diel activity similar to those of summer, indicating less preference for the daylight hours. The greater use of dark hours by these caribou and others on the Seward Peninsula in Alaska (Collins and Smith 1989) suggest that caribou use are better adapted to use sensory cues other than sight (e.g. smelling lichens through the snow) than are sheep, that other forages used in winter, such as willow, are more easily located above the snow than the graminoids sought by sheep, or that the less precipitous terrain inhabited by caribou is less dangerous to negotiate in darkness. Further, although number of hours spent active in early summer was similar for caribou and sheep, caribou spent more time active in both late summer and late winter (Maier and White, in prep.) than did sheep. The elevated activity in late summer for caribou was associated with insect harassment, which sheep living on the higher ridges did not suffer. Greater activity by caribou in late winter, however, could be associated with the high digestibility of lichens in their diet and more rapid digesta passage rates.

Our data were inconclusive regarding the use of moon light for foraging at night, however, in part because ewes were active on nights with no moon, but largely because our sample size for winter was not large enough to separate the confounding effects of

moon phase, variable moon rise and set times, and cloud cover. Because ewes did use similar low light conditions during nautical twilight, we suspect that ewes would also take advantage of moon light for foraging when it was available. Further, the short resting period at midday in winter and the peak of night activity around midnight may have been influenced by gut fill and the necessity of keeping the rumen operating at its maximum. Thus, although Ewes are normally diurnal, they forage at night when conditions necessitate such activity, as do bighorn sheep in the desert during the heat of summer (Krausman et al. 1985).

During the 24-hour days of sunlight in June, bout length for both active and resting behaviors was just over 1 hour suggesting that when sheep feed on green forage, maximum digestion of forage is attained by alternating 1 hour foraging and 1 hour rumination bouts. The longer daytime active bouts and night resting bouts in winter probably reflect the lower efficiency of foraging in dark conditions and an effort by the ewes to take advantage of all of the light hours available.

Factors Affecting Activity

Hoefs and Cowan (1979) also reported windchill to be a significant factor in determining Dall's sheep activity in the Yukon; however, their measure was proportion of the population exposed to the wind, rather than a direct measure of effects of wind on activity levels. As with sheep in the Yukon, we observed ewes both to move onto lee slopes. And ewes generally rested more as windchill levels declined during winter;

however, it was not possible to compare activity at specific windchill levels because our measures were taken at the observer location and sheep may have been exposed to different conditions due to temperature inversions and topography effects on wind. Whether ewes bedded more to reduce heat loss through lowered surface area, or because drifted snow on lee slopes made foraging difficult is unclear. Nevertheless, it appears that the insulative value of the pelage of Dall's sheep is compromised significantly by wind in conjunction with cold temperatures. Although windchill and daylength were the only environmental variables retained in the final ANOVA model using days as the sampling unit; temperature, wind speed, wind gust speed, wind, cloud cover, and presence of sunlight, and civil twilight also were related to activity level. Because of the strong seasonality in the Arctic they were also highly correlated with windchill and daylength and were dropped from the model. This was especially true for ambient temperature and daylength measured by civil twilight rather than sunrise and set.

Because the effect of individual ewe was only significant when individuals with fewer than 6 days of data were included in the model, we believe the difference noted among individual ewes in our initial tests was likely due to small sample sizes for some ewes rather than substantial individual variation. The effect of having a lamb at heel was evident only in August and February. The difference between ewes with and without lambs in February, however, may have resulted from a low sample size of ewes without lambs and our sampling from the 2 ewes without lambs on the coldest single day of that sample period -- windchill was -33 C due to high winds (40 km/hr with gusts to 50

km/hr). Consequently, August may be the most critical time of year energetically for ewes with lambs. August is a time of rapidly declining quality of forage, yet the animals still have high energy requirements for lactation and accumulation of fat reserves for winter.

The strong positive correlations that we observed between most of the nutritional variables tested and hours of activity per day resulted in a high level of intercorrelation among the nutritional variables. FN and IVDMD were the most highly correlated with hours active per day because both are indices to the time required to break down forage and pass digesta from the rumen (Wehausen 1995) -- the primary restriction on forage consumption by ruminants when availability is not limiting (Church 1976). FN was more strongly correlated with hours of activity than was IVDMD in our study, possibly because FN was measured directly from the animals, whereas our method of deriving IVDMD was several steps removed from the animal. These steps included estimating species composition of the diet, correcting for differential digestibility, collecting forage samples to simulate sheep foraging, assembling a simulated diet, and finally digesting the material in vitro. Some of the many assumptions required with these steps were undoubtedly violated to some degree, adding unexplained variation to the data and reducing the statistical correlation. The slight departure of the lines for FN and hours of activity (Fig. 22) during October and December is likely related to windchill and daylength as these continued to decline through this period, as did activity.

Energy Model

Calibration.-- Although IVDMD usually underestimates in vivo digestibility (Milchunas et al. 1978), the values measured for our samples were particularly low. The lowest values for apparent digestibility in a review of domestic sheep and cattle studies was about 42% (Wehausen 1995), yet some of our winter IVDMD results indicated digestibilities of 23-30%, and laboratory personnel described the digestion process as "flat". We suspect the low values resulted from our inability to be as selective in collecting forage samples as were ewes in foraging, storage of forage samples in the air-dried state prior to IVDMD, use of rumen inocula from domestic sheep that were not well adapted to the forages Dall's sheep were consuming, inhibitory effects of secondary compounds which could not be counteracted in the digestion tube as well as in the rumen (Person et al. 1980), or a combination of these. Whatever the cause, only apparent digestibility estimated from FN gave values that yielded the expected model results for winter. Model output, however, indicated that apparent digestibility in summer based on the regression from FN was overestimated. We suspect this was because summer diets of our ewes largely consisted of forbs (46-47%) and shrubs (12-23%) (Chapter 3), which can inflate FN measurements as a result of protein complexing by secondary compounds (Hobbs 1987, Robbins et al. 1987).

Snow cover had a large effect on digestibility of winter diets by restricting availability of forage to the ewes. Our field work took place over approximately 10 days every 2 months, and the measurements taken were assumed to represent the entire period.

Because snow conditions can change rapidly as a result of storms or high wind, it is likely that our measurements of digestibility from each technique showed the range of conditions to which ewes were exposed but not necessarily the average conditions for each bi-monthly period.

The ratio of energy metabolized from fat (81.5%) and protein (18.5%) in our model animal had to be adjusted from that for mule deer (73% fat : 27% protein) (Torbit et al. 1985) to produce the changes in body composition reported for Ewes in the Alaska Range (Heimer 1980). This suggests that accumulation of greater fat reserves is one way that Ewes may be adapted to survive the extreme conditions of winter in the Arctic. Use of energy from fat is much more efficient than from protein, and such an adaptation would allow animals to increase weight gain in summer and reduce weight loss in winter.

Sensitivity analyses.-- The effect of increased digestibility on energy balance and weight gain of the model animal was large because of the multiplier effect (Seip 1983, White 1983). Not only did it affect DE as a proportion of GE, but it affected DMI directly by increasing rumen passage rate. In particular in our case, DMI was the product of digestibility and fecal excretion rate. The reason that digestibility in June was more sensitive to change than in other bi-monthly periods, was that DMI is affected not by digestibility so much as by its complement, indigestibility (Wehausen 1995). Consequently, a 10% increase in digestibility from 75% to 85% would reduce indigestibility by 40% (25% to 15%), whereas in winter a 10% increase in digestibility from 60% to 70% reduces indigestibility by only 25%.

Of the other 2 input variables to which the model was quite sensitive, forage GE did not vary much over a wide variety of forages, but fecal excretion did vary seasonally by nearly a factor of 3. Consequently, our results are consistent with those of Hudson and White (1985) and Fancy (1986) in suggesting that the most important of the model inputs to estimate accurately are digestibility (especially summer) and fecal excretion, or its derivative in our case -- DMI.

Simulation of severe conditions.-- The first series of simulations dealing with reductions in summer digestibility suggested that the model animal would survive a reduction in both June and August digestibility of 5-7% in conjunction with similar reductions in December digestibility, but would not be able to bear young and would be at the 1% body fat level by the following spring when forage conditions improved. The second series of simulations indicated that with reductions due to snow cover in any 3 of the 4 winter bi-monthly periods the model animal would be at the limit of survival after enduring 24-27 days of reliance on protein catabolism to make up deficits in daily energy balance. We can infer that because the model animal represents an average animal, those animals in the population that entered such a winter with below-average energy reserves would die. This equates to a 50% overwinter loss to the ewe population. Such losses occur occasionally throughout Alaska (Murie 1944, Whitten 1975, Nichols 1978); however, no data are available on forage digestibility or DMI of sheep during such a winter with which to compare our results.

The live weights we measured for Ewes in the Brooks Range were considerably higher than those in ewes from 2 populations in central Alaska (Heimer 1980) and 1 in southern Alaska (Nichols 1978) (Fig. 27). The third and fourth series of simulations, in which we changed live weight and percent body fat, suggested that changes in body size without increasing proportion of live weight made up of fat did not change the model animal's ability to endure extended negative energy balance in winter. This was because RMR is a function of weight. Further, weight loss of ewes from the Brooks Range was apparently greater than for more southern populations (Fig. 27). Furthermore, our model suggested that a model animal equivalent in size to those of the Alaska Range but exposed to Brooks Range forage conditions would drop from 14% body fat in October to 9% body fat in 139 days, whereas equivalent fat loss in the Alaska Range took approximately 180 days (Heimer 1980). Such weight loss implies that ewes from the Brooks Range have to begin winter with larger fat reserves than more southern ewes to end the winter in condition to bear a lamb. Thus, greater live weight of ewes from the Brooks Range may be an adaptation to the longer, darker winters above the Arctic Circle, or it could result from a higher proportion of the population not lambing in consecutive years and thus being able to put energy resources into reserves for the next year.

Although Bergmann's Rule relating temperature to body size may be invalid (Geist 1987), Ewes do not respond to shorter duration of the annual forage productivity pulse by having reduced body size with increasing latitude above 60° N. as suggested by Geist (1987) for large mammals in general. Rather it appears that, at least in the range of

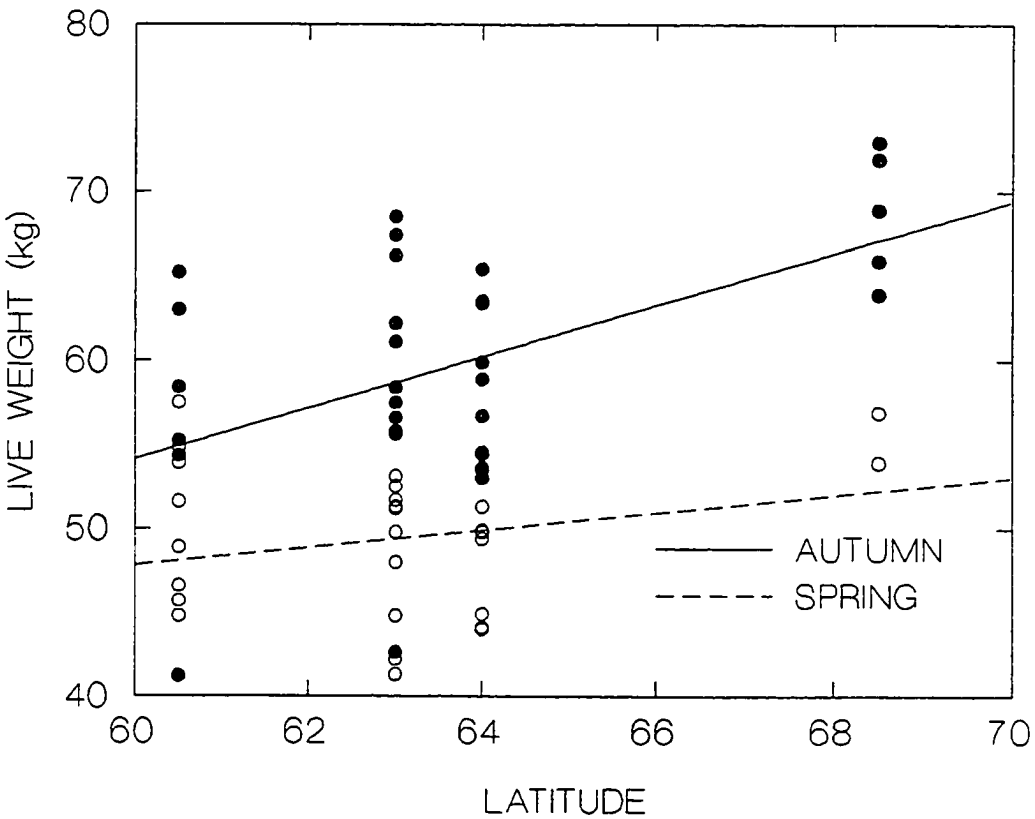

Fig. 27. Relationship of latitude to live weight of adult female Dall's sheep in southern Alaska (Nichols 1978), 2 populations in the Alaska Range of central Alaska (Heimer 1980), and the Brooks Range, Alaska (this study).

60° N. to 70° N., live weight of Ewes increases with latitude. This could be a result of generally increased body size due to improved nutrition in drier, colder climates where plant digestibility tends to increase (Langvatn and Albon 1986), or an adaptation to longer periods of poor nutrition in winter through larger energy reserves, probably in the form of fat. The latter hypothesis appears more likely because total length of Ewes we studied was similar to those from southern Alaska (Nichols 1978). Svalbard reindeer from the high Arctic have adapted to long winter periods similarly by developing large fat reserves (Reimers and Ringberg 1983), however, they are both smaller than more southern caribou and reindeer in both live weight (Reimers and Ringberg 1983) and skeletal size (Klein et al. 1987).

MANAGEMENT IMPLICATIONS

The primary implication from our modeling exercises is that any management action that restricts the ability of Dall's sheep to select the most digestible forage available will reduce the energy reserves these animals have available to endure the long period of negative winter energy balance. These effects will be magnified if confounded by the occasional winter that produces deep or crusted snow. The primary management that occurs in most Dall's sheep ranges is the setting of hunting seasons and limits, because areas inhabited by these animals are generally far removed from most other human activity. Other than direct removal of individuals, the greatest potential effects of hunting are the energy cost of increased movement and displacement from the best foraging areas. The model indicated that the cost of increased movement was negligible, but displacement

from prime foraging areas could in some cases be significant, particularly for females with lambs. The traditional mid-August to mid-September sport hunting season coincides with late lactation and the last chance for these ewes to gain weight before winter. As evidenced by their increased foraging times over those of females without lambs, the traditional hunting season may coincide with a critical time of year females with lambs. Restricted forage availability due to snow cover in August primarily reduced protein content of the diet (Chapter 3). Human disturbance at this time of year can be expected to result in similar reductions in protein intake, which could reduce growth of lambs prior to winter and subsequent lamb survival. This problem should be minimal, as the sexes are usually segregated at this time of year and ram seasons are the rule; however, hunters should be cautioned not to harass females during late summer and early autumn, particularly when using aircraft. Physical changes in the environment through development are unusual in sheep habitat in Alaska, although construction of highways or other transportation corridors occasionally does occur. These should be sited in locations that do not restrict access by sheep to foraging areas, especially those used in winter.

The model, and presumably the ewes, was sensitive to changes in digestibility and DMI. Yet, available techniques for measuring these parameters for wild herbivores give estimates with significant variability and bias. Therefore, when using forage quality measures such as these to index differences among populations or seasons it is important to collect information by multiple techniques and use knowledge of the biases of each technique to derive the best estimates possible. Additional refinement in the measurement

of seasonal digestibility and DMI, or in our case fecal excretion, is needed as well; however, logistical limitations are significant in most field situations.

The bi-monthly periods we used did not allow precise dating of the beginning and end of the large increase in summer digestibility and associated energy intake. Because the peak of intake in summer is so high and so short in duration, small errors in measuring the timing of its initiation and decline could lead to differing conclusions. More frequent field sampling of forage digestibility should occur at these times to increase the resolution of estimates for this time of year.

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SYNOPSIS AND CONCLUSIONS

Use of digestibility correction procedures in conjunction with microhistological analyses is critical to understanding the diets of Dall's sheep in spring and summer when forages with high digestibility are mixed in the diet with other species with lower digestibility. Forbs were far more important in the summer diets of Ewes than many previous studies, which did not use digestibility corrections, had concluded. Consequently, selection indices that indicate Stone sheep do not follow optimal foraging theory by selecting for taxa with the highest protein content in summer (Seip 1983, Seip and Bunnell 1985) are probably invalid. Rather, the results of this study suggest that Ewes did strongly select for highly digestible forbs when they are available; and, therefore, did forage optimally in summer in the northern Brooks Range.

Winter forage available to Dall's sheep in the northern Brooks Range was low in both digestibility and protein content. Further, limited availability of daylight, as well as occasional snow cover on usually wind-swept ridges in winter, limited the ability of these sheep to locate the best available forage. Two apparent adaptations of ewes to these winter conditions above the Arctic Circle are high efficiency of fat deposition and catabolism and larger body size as a result of larger fat reserves. Summer nutrition is important to late winter survival in wild sheep (Hebert 1973) because it allows weight gains to continue into autumn by recycling nitrogen from body reserves (Staaland et al. 1984). This helps to support rumen microflora that most available autumn forage could

not support (Hebert 1973), which is especially important in the northern Brooks Range because most winter forage has low digestible protein for at least 7 months of the year. Further, the multiplier effect (Seip 1983, White 1983) of small gains in digestibility and DMI on weight gain point out the importance of selective foraging for the most nutritious plants and plant parts during the 4-5 months of spring, summer, and autumn when forages with variable protein levels are available. Although size of most populations of Dall's and Stone sheep is probably limited by reduced forage availability resulting from snow cover on winter ranges (Seip 1983, Heimer 1992), these results support the conclusion that forage quality in summer is likely responsible for most differences in body and horn growth rates of sheep in different populations (Whitten 1975, Winters 1980).

Despite a preference for diurnal activity, available daylight in winter did not allow Dall's sheep enough foraging time to keep their rumens full without foraging during darkness. Much of the nocturnal activity occurred during the low light conditions prior to civil twilight in the morning and after civil twilight in the evening, but 2 small peaks of activity occurred around midnight and 0300 hours. Although I suspect that sheep also use moonlight when available, sample sizes were too small to be conclusive. Conversely, in summer sheep were active during all 24 hours of the day, and optimal breakdown and digestion of green forage was apparently attained with alternating 1 hour periods of foraging and rumination. Time spent active per day was closely correlated with FN because it is an index to forage digestibility and thus digesta passage rate, although

windchill and daylength were correlated with activity because sheep preferred to forage during daylight.

The modeling exercises suggested that IVDMD underestimated forage digestibility during all year; although the regression equation used to predict apparent digestibility from FN yielded an overestimate during summer, but accurate results in winter. The model was more sensitive to changes in forage digestibility, particularly in summer, than any other variable, and so accurate estimates of this parameter as well as precise timing of the short summer growing season are essential for predicting weight changes with the model. Finally, calibration of the model suggested that Dall's sheep in the Brooks Range were able to store and mobilize fat reserves more efficiently than mule deer, and simulations of severe winter conditions showed that the larger size attained by Brooks Range sheep over other populations farther south was likely due to greater fat reserves rather than greater overall size.

Any management action that restricts the ability of Dall's sheep to select the most digestible available forage will reduce the energy reserves of these animals for the long period of negative winter energy balance. These effects will be magnified by occasional winter conditions that produce deep or crusted snow. The primary management that occurs in most Dall's sheep ranges is the setting of hunting seasons and limits, because areas inhabited by these animals are generally far removed from human activity other than hunting. Other than direct removal of individuals, the greatest potential effects of hunting are the energy cost of increased movement and displacement from the best foraging areas.

The model indicated that the cost of increased movement was negligible, but displacement from prime foraging areas in some cases could be significant, particularly for females with lambs. The traditional August sport hunting season coincides with late lactation, which may be the critical time of year for these females as evidenced by their increased foraging times over those of females without lambs. This problem should be minimal, as the sexes are usually segregated at this time of year and ram seasons are the rule; however, hunters should be cautioned not to harass females during late summer and early autumn particularly when using aircraft. Physical changes to the environment through development are unusual in sheep habitat in Alaska, although highways or other transportation corridors occasionally occur. These should be sited so as not to prevent access by sheep to preferred foraging areas.

APPENDIX I.

Table of variables and calculations used in spreadsheet model of Dall's sheep energetics. Spreadsheet rows represented days and calculations are listed by column. All calculations were performed for mean data collection date for each of 12 bi-monthly periods over 2 years. Intervening daily values of variables followed by (†) were derived by linear interpolation between bi-monthly values. Variables followed by (‡) were calculated daily from linearly interpolated variables or other formulas. Note that RMR, METWT, and LVWT form a circular calculation, thus, after changing any of these variables the spreadsheet must be recalulated several times until outputs stabilize. Default values are given for the model setpoint -- 23 October 1986.

#	Column	Default Value	Units	Calculation	Source
ENERGY INTAKE CALCULATIONS					
1	FEXCR	0.321	kg/day	Fecal excretion rate	Hansen et al., in prep.
2	DIGEST	63.5	%	Forage digestibility	Hansen and Klein, in prep.
3	DMI†	0.879	kg/day	FEXCR / (1-DIGEST)	
4	GE†	18.9	kJ/gram	Gross energy of the forage	Hansen and Klein, in prep.
5	DE	12.9	kJ/gram	Digestible energy of the forage	Hansen and Klein, in prep.
6	ME†	11.3	kJ/gram	(0.96 ×DE) - 1.13	Moe et al. 1972
7	MEI‡	9.92	MJ/day	DMI × ME	
ENERGY EXPENDITURE CALCULATIONS					
8	EFFMAINT‡	71.2	%	(0.35 × (ME / GE)) + 0.503	AFRC 1993
9	EFFPROD‡	47.1	%	(0.78 × (ME / GE)) + 0.006	AFRC 1993
10	EFFMOBIL	84.0	%	Efficiency of energy mobilization	AFRC 1993
11	METWT	23.9	kg	$LVWT^{0.75}$ of DAY-1	
12	RESTMET	0.418	$MJ/(kg^{0.75}\times day)$	Resting metabolic rate per $kg^{0.75}$ for standing	Chappel and Hudson 1980
13	RMR_{STD}	9.99	MJ/day	METWT × RESTMET	
14	H_{FEED}	9.7	hr	Hours/day sheep spent feeding	This study
15	H_{WALK}	0.2	hr	Hours/day sheep spent walking	This study
16	H_{RUN}	0.02	hr	Hours/day sheep spent running	This study
17	H_{STD}	0.845	hr	Hours/day sheep spent standing	This study
18	H_{LHU}	12.5	hr	Hours/day sheep spent lying with head up	This study
19	H_{LHD}	0.77	hr	Hours/day sheep spent lying with head down	This study
20	I_{FEED}	1.17		Incremental energy cost for feeding over standing	Chappel and Hudson 1980

APPENDIX I. (cont.)

#	Column	Default Value	Units	Calculation	Source
21	I_{WALK}	1.5		Incremental energy cost for walking over standing	Chappel and Hudson 1980
22	I_{RUN}	5		Incremental energy cost for running over standing	Fancy and White 1985
23	I_{STD}	1			
24	I_{LHU}	0.84		Incremental energy cost for lying with head up over standing	Chappel and Hudson 1980
25	I_{LHD}	0.75		Incremental energy cost for lying with head down over standing	Fancy and White 1985
26	EX_{FEED}	4.72	MJ/day	$(RMR_{STD} .\times. I_{FEED}) .\times. (H_{FEED} / 24)$	
27	EX_{WALK}	0.12	MJ/day	$(RMR_{STD} .\times. I_{WALK}) .\times. (H_{WALK} / 24)$	
28	EX_{RUN}	0.04	MJ/day	$(RMR_{STD} .\times. I_{RUN}) .\times. (H_{RUN} / 24)$	
29	EX_{STD}	0.35	MJ/day	$(RMR_{STD} .\times. I_{STD}) .\times. (H_{STD} / 24)$	
30	EX_{LHU}	4.36	MJ/day	$(RMR_{STD} .\times. I_{LHU}) .\times. (H_{LHU} / 24)$	
31	EX_{LHD}	0.24	MJ/day	$(RMR_{STD} .\times. I_{LHD}) .\times. (H_{LHD} / 24)$	
32	EXMAINT†	9.84	MJ/day	$EX_{FEED} + EX_{WALK} + EX_{RUN} + EX_{STD} + EX_{LHU} + EX_{LHD}$	
33	t‡	Non-Preg.	day	Days since conception	
34	E_t‡	Non-Preg.	MJ	$\log_{10}(E_t) = 3.322 - (4.979 \times e^{-0.00643t})$	AFRC 1993
35	W_o	4.0	kg	Lamb weight at birth	AFRC 1993
36	EGEST‡	Non-Preg.	MJ/day	$(0.25 \times W_o) \times [E_t \times (0.07372 \times e^{-0.00643t})]$	AFRC 1993
37	BF	70	g/kg	Butterfat content of milk	AFRC 1993, Chen et al. 1965
38	LACTDAY‡	--	day	Days since parturition	
39	EMILK‡	Non-Lact.	MJ/kg	$(0.0328 \times BF) + (0.0025 \times LACTDAY) + 2.2033$	AFRC 1993
40	YMILK†	Non-Lact.	kg/day	Linear interpolation	AFRC 1993
				LACTDAY: 1, 5, 15, 45, 75, 105 / YMILK: 0.2, 0.75, 1.25, 1.1, 0.7, 0.0	
41	EXTOTAL‡	9.84	MJ/day	EXMAINT + EGEST	
42	EB‡	0.08	MJ/day	MEI - EXTOTAL	
WEIGHT CHANGE CALCULATIONS					
43	ENFAT	39.75	kJ/day	Energy content of fat	AFRC 1993
44	ENPROT	23.85	kJ/day	Energy content of protein	AFRC 1993

APPENDIX I. (cont.)

#	Column	Default Value	Units	Calculation	Source
45	CPTLEAN%H2O	82.2	%	Adjusted by trial and error	van Es 1977
46	CPTLEAN%PROT	17.8	%	Adjusted by trial and error	van Es 1977
47	CPT%PROT	76.8	%	Adjusted by trial and error	Torbit et al. 1985
48	CPT%FAT	23.2	%	Adjusted by trial and error	Torbit et al. 1985
49	WTCPTH2O‡	Non-Preg.	kg	((CPT%FAT × (E_t / 1.09)) / ENPROT) × CPTLEAN%H2O / CPTLEAN%PROT	
50	WTCPTFAT‡	Non-Preg.	kg	(CPT%FAT × (E_t / 1.09)) / ENFAT	
51	WTCPTPROT‡	Non-Preg.	kg	(CPT%PROT × (E_t / 1.09)) / ENPROT	
52	%ASH	4.58	%	Percent ash in LVWT	Fancy 1986
53	WTCPTASH‡	Non-Preg.	kg	%ASH × (WTCPTFAT + WTCPTPROT + WTCPTH2O)	
54	WTCPT‡	Non-Preg.	kg	WTCPTFAT + WTCPTPROT + WTCPTH2O + WTCPTASH	
55	LEAN%H2O	71	%	Percent water in lean tissue	van Es 1977
56	LEAN%PROT	29	%	Percent dry protein in lean tissue	van Es 1977
57	%PROT	18.5	%	Adjusted by trial and error	Torbit et al. 1985
58	%FAT	81.5	%	Adjusted by trial and error	Torbit et al. 1985
59	WTFAT‡			Maternal fat weight	
60	EB>0	9.6	kg	$WTFAT_{DAY-1}$ + ((%FAT × (EB × EFFPROD)) / ENFAT)	
61	EB<0, %FAT>1	--	kg	$WTFAT_{DAY-1}$ + ((%FAT × (EB × EFFMOBIL)) / ENFAT)	
62	EB<0, %FAT<1	--	kg	$WTFAT_{DAY-1}$	
63	WTPROT‡			Maternal dry weight of protein	
64	EB>0	8.7	kg	$WTH2O_{DAY-1}$ + ((%PROT × (EB×EFFPROD)) / ENPROT)	
65	EB<0, %FAT>1	--	kg	$WTH2O_{DAY-1}$ + ((%PROT × (EB×EFFMOBIL)) / ENPROT)	
66	EB<0, %FAT<1	--	kg	$WTH2O_{DAY-1}$ + ((1 × (EB×EFFMOBIL)) / ENPROT)	
67	WTH2O‡			Maternal weight of water	
68	EB>0	47.5	kg	$WTH2O_{DAY-1}$ + (((%PROT × (EB×EFFPROD)) / ENPROT) × LEAN%H2O / LEAN%PROT)	
69	EB<0, %FAT>1	--	kg	$WTH2O_{DAY-1}$ + (((%PROT × (EB×EFFMOBIL)) / ENPROT) × LEAN%H2O / LEAN%PROT)	
70	EB<0, %FAT<1	--	kg	$WTH2O_{DAY-1}$ + (((1 × (EB×EFFMOBIL)) / ENPROT) × LEAN%H2O / LEAN%PROT)	
71	WTASH‡	3.0	kg	%ASH × (WTFAT + WTPROT + WTH2O)	
72	LVWT‡	68.8	kg	WTFAT + WTPROT + WTH2O + WTASH	